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Phylogenetic and morphological studies in *Xylodon* (Hymenochaetales, Basidiomycota) with the addition of four new species

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Abstract

Xylodon (Hymenochaetales, Basidiomycota) is the largest segregate genus of *Hyphodontia* s.l. Based on molecular and morphological data, 77 species are accepted in *Xylodon* to date. Phylogenetic analyses of ITS and 28S sequences, including 38 new ITS and 20 28S sequences of *Xylodon* species, revealed four species new to science. The new taxa *X. exilis*, *X. filicinus*, *X. follis* and *X. pseudolanatus* from Taiwan, Nepal, Réunion, Belize, and USA are described and illustrated. In addition, species concepts for *Odontia vesiculosa* from New Zealand and *Xylodon lanatus* from U.S.A. are revised and the new name *X. vesiculosus* is proposed. Phylogenetic analyses of the ITS region placed *X. spathulatus*, *X. bubalinus* and *X. chinensis* in a strongly supported clade and demonstrated that they are conspecific. *Palifer* and *Odontiopsis* are synonymised under *Xylodon* based on morphological and sequence data. The following new combinations are proposed: *X. erikssonii*, *X. gamundiae*, *X. hjortstamii*, *X. hyphodontinus*, *X. septocystidiatus* and *X. verecundus*. Line drawings of *X. cystidiatus*, *X. hyphodontinus*, *X. lanatus* and *X. vesiculosus*, as well as photographs of *X. raduloides* basidiomata, are provided. A key to *X. lanatus* and similar species is presented.

Keywords

Agaricomycetes, corticioid fungi, Schizoporaceae, *Schizopora*, *Odontia ambigua*, *Xylodon echinatus*

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Introduction

The corticioid fungal genus *Xylodon* (Pers.) Gray, based on the generic type *X. quercinus* (Pers.) Gray, was described in 1801 by Persoon as *Sistotrema* sect. *Xylodon* and belongs in the Hymenochaetales (Basidiomycota). Species of *Xylodon* were usually placed in *Hyphodontia* J. Erikss. until Hjortstam and Ryvarden (2002, 2009) reorganised *Hyphodontia* s.l. into different genera based on morphological features.

The most recent generic description of *Xylodon* was published by Riebesehl and Langer (2017). With few exceptions, the hymenophore in *Xylodon* is odontioid or poroid with many different cystidia types and basidiospore shapes.

Xylodon spp. are primarily wood decomposers, causing a white-rot of angiosperms and gymnosperms (Eriksson and Ryvarden 1976, Yurchenko and Wu 2014). A few species have been collected on brown-rotten spruce stumps, palms or palm tree inflorescences, bamboo, ferns and on the herbaceous *Staehelina dubia* L. and *Fallopia sachalinensis* (F.Schmidt) Ronse Decr. (Burdsall and Nakasone 1981, Langer 1994, Nordén et al. 1999, Kotiranta and Saarenoksa 2000, Boidin and Gilles 2003, Hjortstam et al. 2005, Xiong et al. 2010, Jo et al. 2018). *Xylodon* has a worldwide distribution, with both cosmopolitan species and species restricted to a limited geographic area.

Palifer Stalpers & P.K.Buchanan (1991), based on *Peniophora verecunda* G.Cunn. from New Zealand, is another segregate genus of *Hyphodontia* s.l. recognised by Hjortstam and Ryvarden (2009). It is characterised by encrusted cystidia and remained monotypic until 2007 when three species were transferred to the genus (Hjortstam and Ryvarden 2007a). After a thorough morphological study of *Palifer* species and related taxa, Gorjón (2012) concluded that *Palifer* was probably a synonym of *Xylodon* but did not propose any new combinations. *Palifer* is represented by only one nuclear ribosomal internal transcribed spacer (ITS) sequence in the public record and phylogenetic analyses showed it to be embedded in *Xylodon* (Larsson et al. 2006). Riebesehl and Langer (2017), however, declined to synonymise *Palifer* with *Xylodon* based on one DNA sequence alone and chose to emphasise its morphological features.

Odontiopsis Hjortstam and Ryvarden (1980) is based on the type species *O. hyphodontina* Hjortstam & Ryvarden from Tanzania. It is characterised by an odontioid hymenium, encrusted hyphae projecting from the aculei, stout basidia and globose to subglobose basidiospores. Hjortstam and Ryvarden (1980) mentioned hyphal and basidial similarities with *Schizopora* and *Hyphodontia*.

In this study, we conducted an in-depth phylogenetic study of 36 *Xylodon* species represented by 96 strains or collections, including 58 new ITS and large subunit (28S) ribosomal DNA sequences. Phylogenetic analyses of the ITS and 28S sequence data uncovered four new taxa, *X. exilis*, *X. filicinus*, *X. follis* and *X. pseudolanatus*, that are described and illustrated. In addition, the species complex of *X. spathulatus* was identified and resulted in the synonymisation of two taxa. The genera *Palifer*

and *Odontiopsis* are re-evaluated and placed in synonymy with *Xylodon*, resulting in a number of new combinations. Morphological studies in *Xylodon lanatus* and *Odontia vesiculosa* were conducted and a key to morphologically similar species is provided. Line drawings of *X. cystidiatus*, *X. hyphodontinus* and *X. vesiculosus* are presented and *X. vesiculosus* is described.

Methods

Molecular study

Pieces of dried basidiomata served as material for DNA extractions with the E.Z.N.A.® Fungal DNA Mini Kit (Omega Bio-Tek, VWR, USA). Two nuclear ribosomal DNA markers were used in this study: the ITS region and the D1-D2 domains of 28S. The ITS region includes the internal transcribed spacers 1 and 2 as well as the intercalary 5.8S rRNA gene. For amplification of ITS, different combinations of the following primers were used: ITS1-F (Gardes and Bruns 1993), ITS1, ITS2, ITS3, ITS4, ITS5 (White et al. 1990) and ALR0 (Collopy et al. 2001). The last one was modified in one position (Riebesehl and Langer 2017). NL1, NL4 (O'Donnell 1993), LR0R (Bunyard et al. 1996) and LR5 (Vilgalys and Hester 1990) were used, also in different combinations, for the amplifications of the D1-D2 domains of 28S. PCR products were purified with innuPREP PCRpure Kit (Analytik Jena, Berlin, Germany) and the DNA sequencing was implemented by Eurofins Genomics (Ebersberg, Germany).

Newly generated sequences were edited with MEGA7 (Kumar et al. 2016). Their quality was checked following the five guidelines by Nilsson et al. (2012) and they were deposited in NCBI GenBank (Benson et al. 2018; Tab. 1). Other sequences used in this study were downloaded from the same database. *Phellinus gabonensis* Decock & Yombiyeni (Hymenochaetales) was chosen as the outgroup for rooting the phylograms. The two different alignments were calculated with MAFFT v.7 (Katoh and Standley 2013), using the L-INS-i algorithm for ITS and G-INS-i for 28S. Minimum Evolution (ME) and Bayesian inference (BI) trees were calculated for both datasets. The ME phylograms were computed with MEGA7, using the Tamura-Nei model (Tamura and Nei 1993) including 1000 bootstrap (BS) replications, partial deletion of gapped positions with 95% site coverage cut-off and other default settings. The BI phylograms were constructed with MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003), using DNA substitution models estimated by MrModeltest 2.4 (Nylander 2004) with 10 million generations and one tree saved for every 1000 generations; other parameters used default settings. A partitioned analysis was done for the ITS alignment with independent DNA substitution models and parameter values for ITS1, 5.8S and ITS2. MEGA7 and FigTree 1.4.2 (Rambaut 2012) were used for processing the phylograms.

Table 1. List of accepted species in *Xylodon* with some closely related species from other genera, including specimens used in the phylogenetic study. Newly generated sequences are shown in bold. *Xylodon* species without available ITS or 28S sequences are marked with 'not available' (n.a.); these have to date not been studied using ribosomal sequence data.

Species	Specimen voucher	GenBank accession number		Reference	Country
		ITS	28S		
Hastodontia hastata (Litsch.) Hjortstam & Ryvarden	KAS-GEL3124	DQ340311	–	unpublished	Sweden
	EL47/99 (GB)	–	DQ873620	Larsson et al. 2006	Sweden
***Hyphodontia borbonica* Riebesehl, Langer & Barniske**	**FR-0219441, Holotype**	KR349240	–	Riebesehl et al. 2015	**Réunion**
	–	–	**MH884915**	**This study**	–
H. pallidula (Bres.) J.Erikss.	KAS-GEL2097	DQ340317	DQ340372	unpublished	Germany
Kneiffiella barba-jovis (Bull.) P.Karst.	KHL 11730 (GB)	DQ873609	DQ873610	Larsson et al. 2006	Sweden
K. palmae Rick ex Hjortstam & Ryvarden	FR7	KP689185	–	Wang et al. 2016	China
	KAS-GEL3456	–	DQ340369	unpublished	Taiwan
Lagarobasidium calongei M.Dueñas, Tellería, Melo & M.P.Martín	MA-Fungi 73256	NR119737	n.a.	Dueñas et al. 2009	Azore Islands
Lyomyces crustosus (Pers.) P.Karst.	TASM YG-G39	MF382993	–	Gafforov et al. 2017	Uzbekistan
	KAS-GEL2325	–	DQ340354	unpublished	Germany
L. sambuci (Pers.) P.Karst.	KAS-JR7	KY800402	KY795966	Yurchenko et al. 2017	Germany
Phellinus gabonensis Decock & Yombiyeni	MUCL 52025	HM635715	HM635690	Yombiyeni et al. 2011	Gabon
Xylodon adhaerisporus (Langer) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. anmashanensis (Yurchenko, H.X.Xiong & Sheng H.Wu) Riebesehl, Yurchenko & Langer	–	n.a.	n.a.	–	–
X. apacheriensis (Gilb. & Canf.) Hjortstam & Ryvarden	Canfield 180, Holotype	KY081800	n.a.	Riebesehl and Langer 2017	USA, Arizona
X. archeri (Berk.) Kuntze	–	n.a.	n.a.	–	–
X. asperus (Fr.) Hjortstam & Ryvarden	UC2023169	KP814365	–	Rosenthal et al. 2017	USA, Montana
	KHL8530 (GB)	–	AY586675	Larsson et al. 2004	Sweden
X. astrocystidiatus (Yurchenko & Sheng H.Wu) Riebesehl, Yurchenko & Langer	Wu 9211-71	JN129972	JN129973	Yurchenko and Wu 2014	Taiwan
***X. australis* (Berk.) Hjortstam & Ryvarden**	**CIEFAP-11041 (CFMR)**	n.a.	**MH884895**	**This study**	**Argentina**
X. bisporus (Boidin & Gilles) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. borealis (Kotir. & Saaren.) Hjortstam & Ryvarden	UC2022850	KP814307	–	Rosenthal et al. 2017	USA, Connecticut
	JS26064	–	AY586677	Larsson et al. 2004	Norway
X. bresinskyi (Langer) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. brevisetus (P. Karst.) Hjortstam & Ryvarden	KHL 12386 (GB)	DQ873612	DQ873612	Larsson et al. 2006	Sweden
X. bubalinus (Min Wang, Yuan Y. Chen & B.K. Cui) C.C. Chen & Sheng	CLZhao 184	MG231628	n.a.	unpublished	China
	Cui 6834	KY290981	–	Wang and Chen 2017	China
	Cui 12887	KY290982	–	Wang and Chen 2017	China
	Cui 12888, Holotype	KY290983	–	Wang and Chen 2017	China
X. candidissimus (Berk. & M.A.Curtis) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. capitatus (G.Cunn.) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–

Species	Specimen voucher	GenBank accession number		Reference	Country
		ITS	28S		
X. chinensis (C.C.Chen & Sheng H.Wu) C.C.Chen & Sheng H.Wu	Wu 1307-42	KX857802	–	Chen et al. 2017	China
	Wu 1407-105, Holotype	KX857804	KX857811	Chen et al. 2017	China
X. crassihyphus (Douanla-Meli) Riebesehl & Langer	–	n.a.	n.a.	–	–
X. crassisporus (Gresl. & Rajchenb.) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. crustosoglobosus (Hallenb. & Hjortstam) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
***X. cystidiatus* (A.David & Rajchenb.) Riebesehl & Langer**	**FR-0249200**	**MH880195**	**MH884896**	**This study**	**Réunion**
X. detriticus (Bourdot) Tura, Zmitr., Wasser & Spirin	UC2023108	KP814412	n.a.	Rosenthal et al. 2017	USA, Michigan
X. echinatus (Yurchenko & Sheng H.Wu) Riebesehl, Yurchenko & Langer	–	n.a.	n.a.	–	–
X. erikssonii (M.Galán & J.E.Wright) Riebesehl & Langer	–	n.a.	n.a.	–	–
***X. exilis* Yurchenko, Riebesehl & Langer**	**MSK-F 7381**	**MH880196**	–	**This study**	**Taiwan**
	MSK-F 7431	–	**MH884897**	**This study**	**Taiwan**
	TUB-FO 42450	**MH880197**	–	**This study**	**Taiwan**
	TUB-FO 42565, Holotype	**MH880198**	**MH884898**	**This study**	**Taiwan**
***X. filicinus* Yurchenko & Riebesehl**	**MSK-F 12869, Holotype**	**MH880199**	**MH884899**	**This study**	**Taiwan**
	MSK-F 12870	**MH880200**	**MH884900**	**This study**	**Taiwan**
X. fimbriatus (Sheng H.Wu) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
***X. flaviporus* (Berk. & M.A.Curtis ex Cooke) Riebesehl & Langer**	FCUG 1053	AF145575	–	Paulus et al. 2000	Romania
	FR-0249797	**MH880201**	**MH884901**	**This study**	**Réunion**
	KAS-GEL3462	**MH880202**	–	**This study**	**Taiwan**
	KAS-GEL5047	**MH880203**	–	**This study**	**Réunion**
	KUC20130808-17	–	KJ668314	Jang et al. 2016	South Korea
***X. follis* Riebesehl, Yurchenko & Langer**	**FR-0249814, Holotype**	**MH880204**	**MH884902**	**This study**	**Réunion**
X. gamundiae (Gresl. & Rajchenb.) Riebesehl & Langer	–	n.a.	n.a.	–	–
X. gracilis (Hjortstam & Ryvarden) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. hallenbergii (Sheng H.Wu) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. hastifer (Hjortstam & Ryvarden) Hjortstam & Ryvarden	Ryvarden 19767, Holotype	KY081801	n.a.	Riebesehl and Langer 2017	Argentina
X. heterocystidiatus (H.X.Xiong, Y.C.Dai & Sheng H.Wu) Riebesehl, Yurchenko & Langer	Wu 9209-27	JX175045	–	Yurchenko and Wu 2014	Taiwan
	–	–	KX857821	Chen et al. 2017	–
X. hjortstamii (Gresl. & Rajchenb.) Riebesehl & Langer	–	n.a.	n.a.	–	–
***X. hyphodontinus* (Hjortstam & Ryvarden) Riebesehl, Yurchenko & G.Gruhn**	**KAS-GEL9222**	**MH880205**	**MH884903**	**This study**	**Kenya**
	LIP GG-GUY13-044	**MH880206**	**MH884904**	**This study**	**French Guyana**
	LIP GG-MAR12-238	**MH880207**	**MH884905**	**This study**	**Martinique**
	LIP GG-MAR15-127	**MH880208**	**MH884906**	**This study**	**Martinique**
X. knysnanus (Van der Byl) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. lanatus (Burds. & Nakasone) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. lenis Hjortstam & Ryvarden	Wu0808-32	–	KX857820	Chen et al. 2017	Taiwan
	Wu890714-3, Holotype	KY081802	–	Riebesehl and Langer 2017	Taiwan

Species	Specimen voucher	GenBank accession number		Reference	Country
		ITS	28S		
X. lutescens (Hjortstam & Ryvarden) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. mollissimus (L.W.Zhou) C.C.Chen & Sheng H.Wu	LWZ20160318-3	KY007517	n.a.	Kan et al. 2017	China
X. mussooriensis Samita, Sanyal & Dhingra	–	n.a.	n.a.	–	–
***X. nespori* (Bres.) Hjortstam & Ryvarden**	KAS-GEL3158	–	DQ340346	unpublished	Sweden
	KAS-JR14	**MH880210**	–	**This study**	**Germany**
	KUC20161012-50	MF774797	–	unpublished	South Korea
X. nesporina (Hallenb. & Hjortstam) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
***X. niemelaei* (Sheng H.Wu) Hjortstam & Ryvarden**	Dai 15358	KT989973	–	Chen et al. 2016	China
	FR-0219860	**MH880211**	–	**This study**	**Réunion**
	FR-0249174	**MH880212**	–	**This study**	**Réunion**
	FR-0249178	–	**MH884907**	**This study**	**Réunion**
	FR-0249225	**MH880213**	–	**This study**	**Réunion**
	FR-0249289	**MH880214**	–	**This study**	**Réunion**
	FR-0249744	**MH880215**	–	**This study**	**Réunion**
	FR-0249811	**MH880216**	–	**This study**	**Réunion**
	FR-0249846	**MH880217**	–	**This study**	**Réunion**
	GC 1508-146	KX857798	–	Chen et al. 2017	Taiwan
	KAS-GEL4904	**MH880218**	–	**This study**	**Réunion**
	KAS-GEL4998	EU583422	–	unpublished	Réunion
	Wu1010-62	–	KX857817	Chen et al. 2017	Taiwan
X. nongravis (Lloyd) C.C.Chen & Sheng H.Wu	GC1412-22	KX857801	KX857818	Chen et al. 2017	Taiwan
X. nothofagi (G.Cunn.) Hjortstam & Ryvarden	PDD:91630	GQ411524	–	Fukami et al. 2010	New Zealand
X. nudisetus (Warcup & P.H.B.Talbot) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. ovisporus (Corner) Riebesehl & Langer	ICMP 13830	AF145584	–	Paulus et al. 2000	New Zealand
	KAS-GEL3493	EU583421	–	unpublished	Taiwan
	KUC20130725-29	–	KJ668365	Jang et al. 2016	South Korea
X. papillosus (Fr.) Riebesehl, Yurchenko & Langer	–	n.a.	n.a.	–	–
***X. paradoxus* (Schrad.) Chevall.**	FCUG 2425	AF145571	–	Paulus et al. 2000	Russia
	KAS-GEL2511	–	AF518647	Hibbett and Binder 2002	Germany
	KAS-JR06	**MH880219**	–	**This study**	**Germany**
	KAS-JR28	–	**MH884908**	**This study**	**Austria**
X. pelliculae (H.Furuk.) Riebesehl, Yurchenko & Langer	–	n.a.	n.a.	–	–
X. poroideoefibulatus (Sheng H.Wu) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. pruniaceus (Hjortstam & Ryvarden) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
***X. pseudolanatus* Nakasone, Yurchenko & Riebesehl**	**FP-150922 (CFMR), Holotype**	**MH880220**	**MH884909**	**This study**	**Belize**
X. pseudotropicus (C.L.Zhao, B.K.Cui & Y.C.Dai) Riebesehl, Yurchenko & Langer	Dai 10768	KF917543	n.a.	Zhao et al. 2014	China
X. quercinus (Pers.) Gray	Otto Miettinen 15050,1 (H 6013352)	KT361632	–	Ariyawansa et al. 2015	Finland
	KHL11076 (GB)	KT361633	AY586678	Larsson et al. 2004	Sweden
***X. raduloides* (Pers.) Riebesehl & Langer**	ICMP 13833	AF145580	–	Paulus et al. 2000	Australia
	KAS-JR 02	**MH880221**	–	**This study**	**Germany**
	KAS-JR 03	**MH880222**	–	**This study**	**Germany**
	KAS-JR 09	**MH880223**	–	**This study**	**Germany**

Species	Specimen voucher	GenBank accession number		Reference	Country
		ITS	28S		
***X. raduloides* (Pers.) Riebesehl & Langer**	**KAS-JR 10**	**MH880224**	–	**This study**	**Germany**
	KAS-JR 26	**MH880225**	**MH884910**	**This study**	**Germany**
	LR 18813	**MH880226**	**MH884911**	**This study**	**Australia**
X. ramicida Spirin & Miettinen	Viacheslav Spirin 7664 (H), Holotype	KT361634	n.a.	Ariyawansa et al. 2015	Russia
X. reticulatus (C.C.Chen & Sheng H.Wu) C.C.Chen & Sheng H.Wu	GC1512-1	KX857808	KX857813	Chen et al. 2017	Taiwan
	KUC20160721B-26	MF774798	–	Kwon et al. 2018	South Korea
	Wu1109-178, Holotype	KX857805	–	Chen et al. 2017	Taiwan
X. rhizomorphus (C.L.Zhao, B.K.Cui & Y.C.Dai) Riebesehl, Yurchenko & Langer	Dai 12354	KF917544	n.a.	Zhao et al. 2014	China
	Dai 12367, Holotype	KF917545	–	Zhao et al. 2014	China
	Dai 12389	KF917546	–	Zhao et al. 2014	China
X. rickii (Hjortstam & Ryvarden) K.H. Larss.	–	n.a.	n.a.	–	–
X. rimosissimus (Peck) Hjortstam & Ryvarden	Ryberg 021031 (GB)	DQ873627	DQ873628	Larsson et al. 2006	Sweden
X. rudis (Hjortstam & Ryvarden) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. septocystidiatus (H.X.Xiong, Y.C.Dai & Sheng H.Wu) Riebesehl & Langer	–	n.a.	n.a.	–	–
***X. serpentiformis* (Langer) Hjortstam & Ryvarden**	**KAS-GEL3668**	**MH880227**	–	**This study**	**Taiwan**
	TUB-FO 40675	**MH880228**	–	**This study**	**Taiwan**
	TUB-FO 40985	–	**MH884912**	**This study**	**Taiwan**
	TUB-FO 42688	**MH880229**	**MH884913**	**This study**	**Taiwan**
X. sp. 1	Dai 15321	KT989969	n.a.	Chen et al. 2016	China
***X. spathulatus* (Schrad.) Kuntze**	KAS-GEL2690	KY081803	–	Riebesehl and Langer 2017	Germany
	KAS-MMS7224	**MH880230**	–	**This study**	**Czech Republic**
	KHL7085 (GB)	KY081804	–	Riebesehl and Langer 2017	Sweden
	MSK-F 12931	**MH880231**	**MH884914**	**This study**	**Russia**
***X. subclavatus* (Yurchenko, H.X.Xiong & Sheng H.Wu) Riebesehl, Yurchenko & Langer**	**TUB-FO 42167**	**MH880232**	n.a.	**This study**	**Taiwan**
***X. subflaviporus* C.C.Chen & Sheng H.Wu**	**KAS-GEL3466**	**MH880233**	–	**This study**	**Taiwan**
	Wu 0809-76	KX857803	KX857815	Chen et al. 2017	China
X. subglobosus Samita, Sanyal & Dhingra	–	n.a.	n.a.	–	–
X. submucronatus (Hjortstam & Renvall) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. subscopinellus (G.Cunn.) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. subtropicus (C.C.Chen & Sheng H.Wu) C.C.Chen & Sheng H.Wu	Wu 1508-2	KX857806	KX857812	Chen et al. 2017	China
	Wu 9806-105, Holotype	KX857807	KX857809	Chen et al. 2017	Vietnam
X. syringae (Langer) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. taiwanianus (Sheng H.Wu) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. tenellus Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. tenuicystidius (Hjortstam & Ryvarden) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. trametoides (Núñez) Riebesehl & Langer	–	n.a.	n.a.	–	–
X. tuberculatus (Kotir. & Saaren.) Hjortstam & Ryvarden	–	n.a.	n.a.	–	–
X. verecundus (G.Cunn.) Yurchenko & Riebesehl	KHL 12261 (GB)	DQ873642	n.a.	Larsson et al. 2006	USA
X. vesiculosus Yurchenko, Nakasone & Riebesehl	–	n.a.	n.a.	–	–

Morphological study

The studied specimens are deposited in herbaria CFMR, FR, KAS, LIP, MSK, and TUB (acronyms follow Index Herbariorum, http://sweetgum.nybg.org/science/ih). Morphological descriptions and figures employed dried basidiomata. Preparations in 3% potassium hydroxide (KOH) aqueous solution were used for microscopic measurements and most drawings. Crystalline deposits on hyphae were additionally examined in Melzer's reagent (Mz) and tap water. Amyloid and dextrinoid reactions of basidiospores were tested with Mz. Spore wall cyanophily was determined in Cotton Blue-Lactophenol solution (CBL). The following abbreviations are used to describe arithmetic averages for 30 basidiospores, randomly selected in squash preparations of one specimen: L – spore length, W – spore width, Q = length/width ratio.

Results

Phylogeny

The aligned ITS data matrix consisted of 92 taxa and 847 positions. The partial deletion of gapped positions resulted in 463 positions that were used in the ME phylogenetic analysis. The data matrix was partitioned as follows: ITS1 = positions 1–373, 5.8S rRNA gene = 374–541 and ITS2 = 542–847. The GTR + G model was used as DNA substitution model for ITS1 and ITS2 and SYM + I for 5.8S in the BI analysis. The aligned data matrix of the D1-D2 domains of 28S rRNA gene consisted of 47 taxa and 634 positions; 532 positions were used in the ME analysis. The GTR + I + G model was chosen as the DNA substitution model for the BI analysis. A high degree of agreement was observed between the ME and BI trees; therefore, the ME phylogram with BS and integrated posterior probability (PP) values from the BI phylogram are presented in Figures 1, 2. The sum of branch lengths in the resulting ME phylograms was 3017 for ITS (Fig. 1) and 1009 for 28S (Fig. 2). Multiple sequence alignments and trees are deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S23512).

The ITS phylogram (Fig. 1) shows a number of clades with low BS support which is well-documented for *Xylodon* (see Chen et al. 2018, Riebesehl and Langer 2017). Figure 1 includes 83 sequences of *Xylodon* specimens or strains of which 38 were generated in this study. No significant distances were observed amongst sequences of *X. niemelaei*, *X. rhizomorphus*, and *X. reticulatus* nor amongst sequences of *X. spathulatus*, *X. chinensis*, and *X. bubalinus*. The strong BS (99 and 97) and PP (1) values of these two clades indicate that the taxa within each clade may be conspecific. Seven collections of *X. raduloides* form two distinct subclades (96 and 98 BS). Similarly, four collections of *X. flaviporus* formed two subclades (99 and 93 BS). The newly generated ITS sequences show that *X. cystidiatus*, *X. hyphodontinus*, *X. serpentiformis* and *X. subclavatus* form distinct lineages in *Xylodon*. The four new species introduced herein form

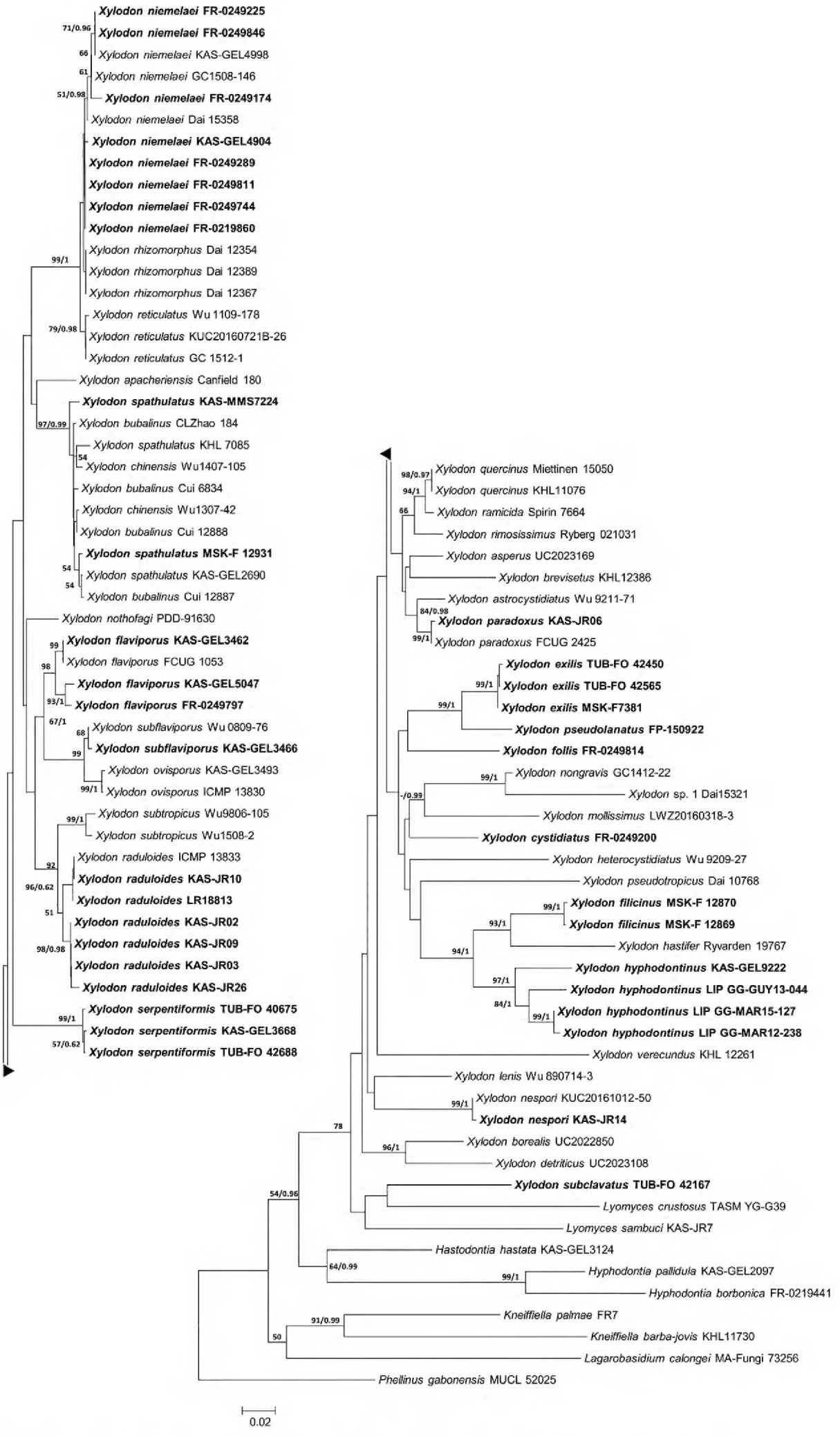

Figure 1. ITS-based Minimum Evolution phylogram for *Xylodon* and allied species. Bootstrap values >50 are shown next to the branches. The second number, if present, represents posterior probabilities received from BI analysis. Scale bar indicates estimated number of substitutions per site. Sequences generated in this study are shown in bold. Voucher numbers and species names are indicated in Table 1.

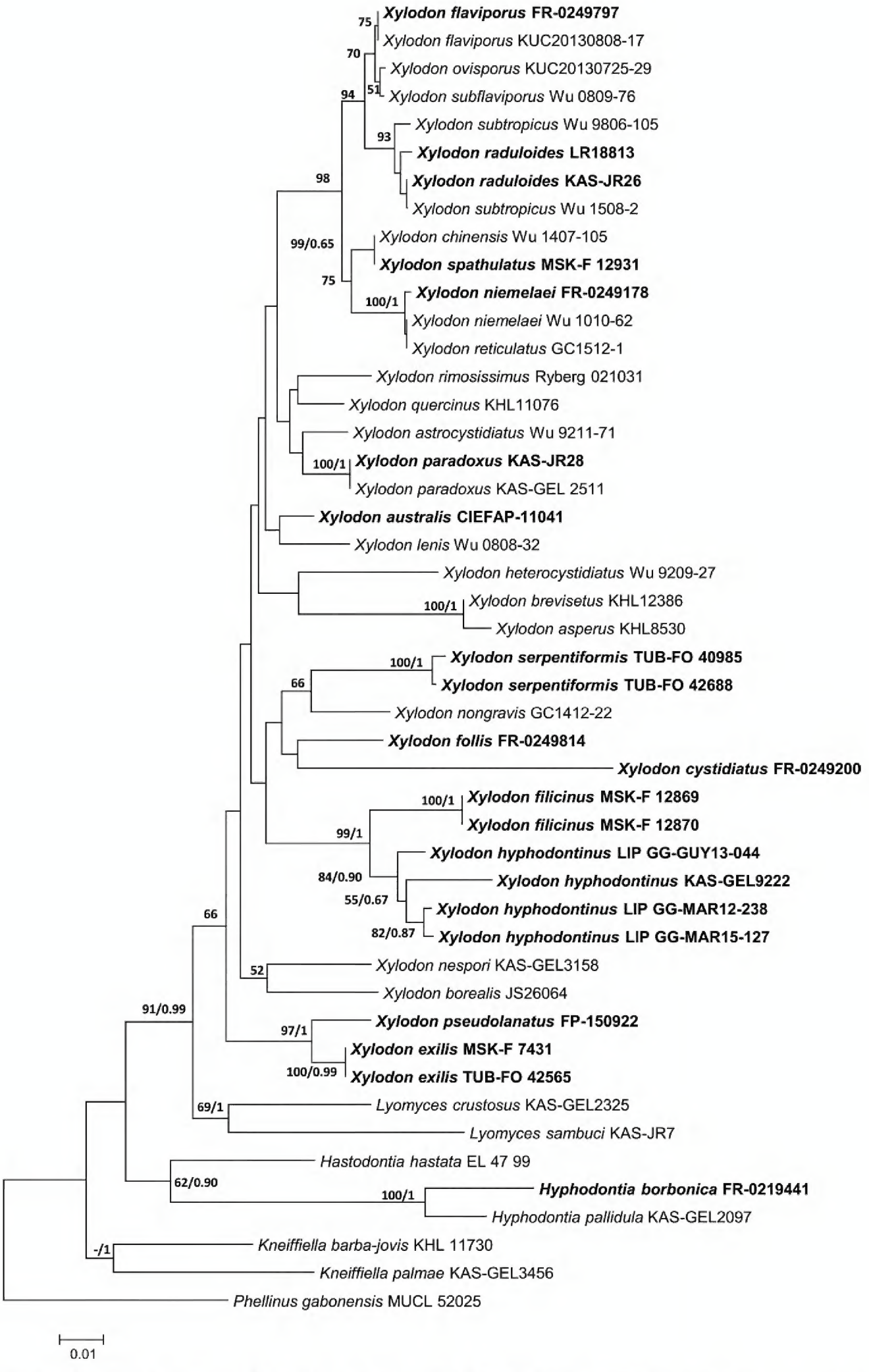

Figure 2. 28S-based Minimum Evolution phylogram for *Xylodon* and allied species. Bootstrap values >50 are shown next to the branches. The second number, if present, represents posterior probabilities received from BI analysis. Scale bar indicates estimated number of substitutions per site. Sequences generated in this study are shown in bold. Voucher numbers and species names are indicated in Table 1.

distinct lineages as well. *Xylodon pseudolanatus* and *X. exilis* are sister groups with 5.9% differences between their ITS sequences (*X. pseudolanatus*: FP-150922 and *X. exilis*: TUB-FO 42565). They cluster in a well-supported clade (99 BS), within a weakly supported lineage that includes *X. follis*. The closest relative of *X. filicinus* is *X. hastifer*; they form a clade (93 BS) that is sister to *X. hyphodontinus* s.l.

The 28S phylogram (Fig. 2) includes 39 sequences of *Xylodon* of which 20 were generated here. Notable new 28S sequences include *X. australis*, *X. hyphodontinus*, *X. serpentiformis*, the four new species described herein, and furthermore *Hyphodontia borbonica*. As the 28S phylogram features several lineages with low BS support, the clades between the 28S and ITS trees are not identical throughout. Although clearly resolved with ITS sequences, the 28S gene analyses were not able to resolve the closely related *X. raduloides* and *X. subtropicus*. Some clades that were well supported with ITS sequences were also well supported in the 28S phylogram, for example, the *X. niemelaei* and *X. reticulatus* (100 BS) and the *X. chinensis* and *X. spathulatus* (99 BS) clades.

Morphology

***Xylodon exilis* Yurchenko, Riebesehl & Langer, sp. nov.**
MycoBank MB827462
Figs 3a, 4

Holotype. TAIWAN, Nantou county, south from Sun-Moon Lake, near Hua Lien, Lien-Hwa-Chi, 700 m a.s.l., on fallen angiosperm twig, leg. E. Langer, G. Langer, F. Oberwinkler, 10 Jul 1990 (TUB-FO 42565; isotypes in KAS and MSK).

Description. Basidiomata effused, 1–5 cm in extent, membranaceous, discontinuous at the periphery. Hymenial surface minutely odontioid, cream-coloured, between aculei 50–130 µm thick. Aculei peg-like, conical or subcylindrical, entire or slightly penicillate apically, 35–70 µm long, 15–50(–70) µm diam., 8–14/mm. Margin abrupt or somewhat thinning out. Hyphal system monomitic, hyphae colourless, with clamps at all primary septa. Subicular hyphae forming a loose tissue, rarely branched, 3–4(–4.5) µm wide, with slightly thick to thick walls (0.5–1.2 µm thick), with scattered adventitious septa, smooth. Subhymenial hyphae in a dense tissue, richly branched, 2–3 µm wide, thin-walled, smooth or slightly encrusted. Capitate cystidia enclosed, 18–22 × 5.5–8 µm, sometimes with an adventitious septum in stem, thin- to slightly thick-walled. Projecting hyphae in aculei flexuous, apically obtuse, 90–130 µm long, 3–4 µm wide, originating from thick-walled subicular hyphae, with simple and clamped septa, often constricted at septa, walls thickened at base then gradually thinning toward apex, moderately encrusted. Basidioles clavate or bowling pin-shaped, 10–20 × 4.5–5.5 µm. Basidia narrowly utriform, 20–25 × 4–5(–5.5) µm, thin-walled, smooth, with four sterigmata 2–4 × 0.3 µm. Spores narrowly ellipsoid, 5.5–6 × 2.5–3 µm, holotype L = 5.8 µm, W = 2.8 µm, Q = (1.6–)1.8–2.2, colourless, smooth, slightly thick-walled, negative in Mz, acyanophilous, with minute apiculus.

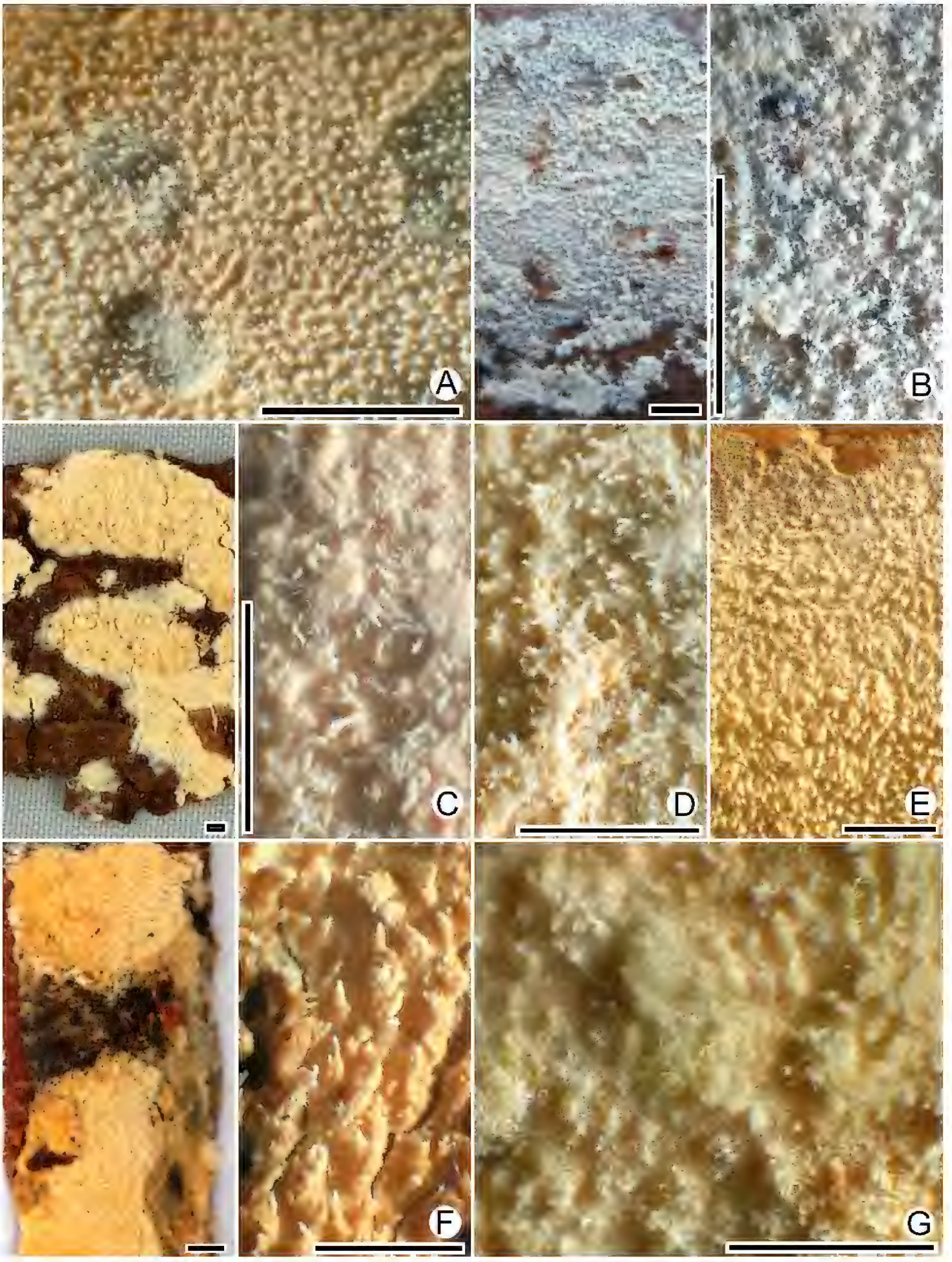

Figure 3. Basidiomata of *Xylodon* spp. **A** *X. exilis* (TUB-FO 42565, holotype) **B** *X. filicinus* (MSK-F 12369, holotype) **C** *X. follis* (FR-0249814, holotype) **D** *X. pseudolanatus* (FP-150922, holotype) **E** *X. pseudolanatus* (HHB-6925, paratype) **F** *X. vesiculosus* (PDD-18112, isotype) **G** *X. lanatus* (CFMR HHB-8925, holotype). Scale bars: 1 mm.

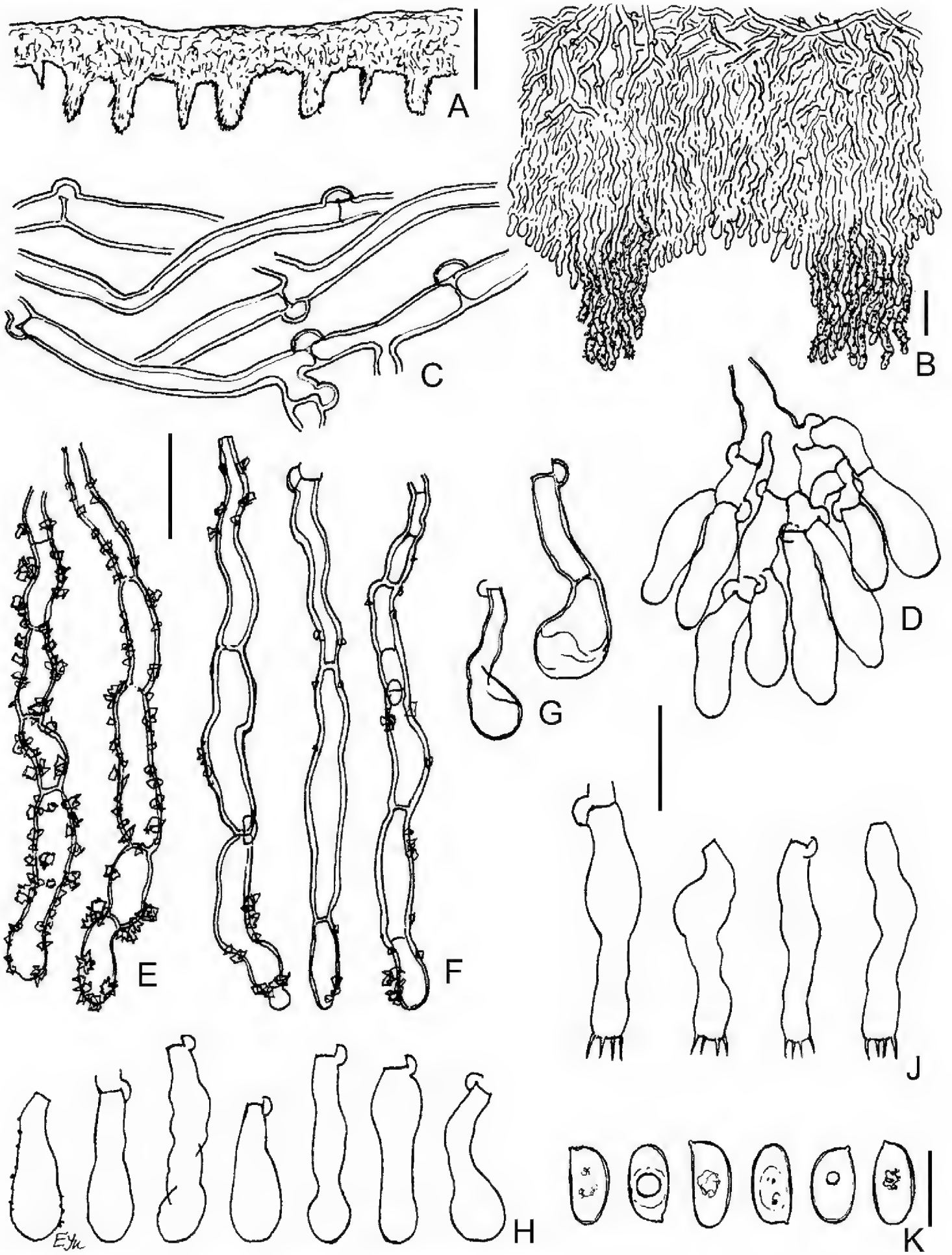

Figure 4. Micromorphology of *Xylodon exilis* (TUB-FO 42565, holotype): **A, B** vertical sections through basidioma **C** subicular hyphae **D** portion of hymenium and subhymenium **E** projecting aculeal hyphae in Mz **F** projecting aculeal hyphae in 3% KOH **G** capitate cystidia **H** basidioles **J** basidia **K** basidiospores. Scale bars: 100 µm (**A**); 20 µm (**B**); 10 µm (**C–J**); 5 µm (**K**).

Distribution and ecology. The species is known from Taiwan and Nepal. It grows on dead wood of angiosperms, with a preference for small branches and twigs.

Etymology. from Latin *exilis* – thin, fine, refers to the small and narrow aculei.

Additional specimens examined. TAIWAN, Nantou Co., west from Sun-Moon Lake, near Hua Lien, on dead wood, leg. E. Langer, G. Langer, F. Oberwinkler, 26 Mar 1989 (TUB-FO 40734; dupl. in KAS); south from Sun-Moon Lake, near Hua Lien, on fallen angiosperm twig, leg. E. Langer, G. Langer, F. Oberwinkler, 9 Jul 1990 (TUB-FO 42450; dupl. in KAS and MSK); Taichung Co., Shinshe, on fallen angiosperm twig, leg. E. Yurchenko, 2 Apr 2011 (MSK-F 12912); ibid., on fallen liana stem, leg. E. Yurchenko, 2 Apr 2011 (MSK-F 12913); ibid., on fallen angiosperm twig, leg. E. Yurchenko, 5 Jun 2011 (MSK-F 12914); Taipei Co., Wulai, Neidong Recreation Area, on fallen angiosperm twig, leg. E. Yurchenko, 23 Jun 2011 (MSK-F 7381; dupl. in KAS and LE); Miaoli Co., Sanyi, on fallen angiosperm branch, leg. E. Yurchenko, 3 Jul 2011 (MSK-F 7431); ibid., on fallen angiosperm branch, leg. E. Yurchenko, 19 Jul 2011 (MSK-F 7430). NEPAL: Gandaki Prov., Kuldi, Anapurna Trek, leg. L. Ryvarden, 7 Nov 1979 (O-LR 18918/B, dupl. in KAS).

Remarks. The species concept of *X. lanatus* is revised and restricted to specimens with a well-developed woolly subiculum. The distinctive characters of *X. exilis* are the minutely odontioid basidiomata with peg-like aculei composed of flexuous, encrusted, septate projecting hyphae that are constricted at the septa, embedded capitate cystidia and narrowly ellipsoid spores with slightly thickened walls. Earlier specimens of *X. exilis* from Taiwan (e.g. Langer 1994, p. 143 for illustration) and Nepal (Hjortstam and Ryvarden 1984) were originally identified as *X. lanatus*. Hyphae and spores of this species were also depicted by Yurchenko et al. (2013) under the name *X. lanatus*. These two species and other morphologically similar taxa are compared in the Discussion section below; a key is also presented.

Xylodon filicinus Yurchenko & Riebesehl, sp. nov.

MycoBank MB827463

Figs 3b, 5

Holotype. TAIWAN, Nantou Co., Xitou (Shitou) Forest Recreation Area, W slope of Phoenix Mt. Range, 1470 m a.s.l., 23°40'N, 120°48'E, old-growth sparse broadleaf forest, on dead detached rachis of *Cyathea* sp., leg. E. Yurchenko, 31 Jul 2011 (field No. 38; MSK-F 12869; isotype in KAS).

Description. Basidiomata effused, white, 2–4 cm in extent, farinaceous or pruinose, very loose or discontinuous, odontioid, 30–55 µm thick between aculei. Margin thinning out. Aculei conical or subcylindrical, 40–80 µm long, 15–45 µm diam., peg-like, of loose texture, 8–14/mm. Hyphal system monomitic, hyphae colourless, clamped at all septa. Subicular hyphae in a loose tissue, rarely branched, 2–3 µm diam., thin- or slightly thick-walled, loosely encrusted, under the subhymenium with inflations 5–6.5 µm wide. The largest crystals in subiculum 6–8 µm across, aggregated

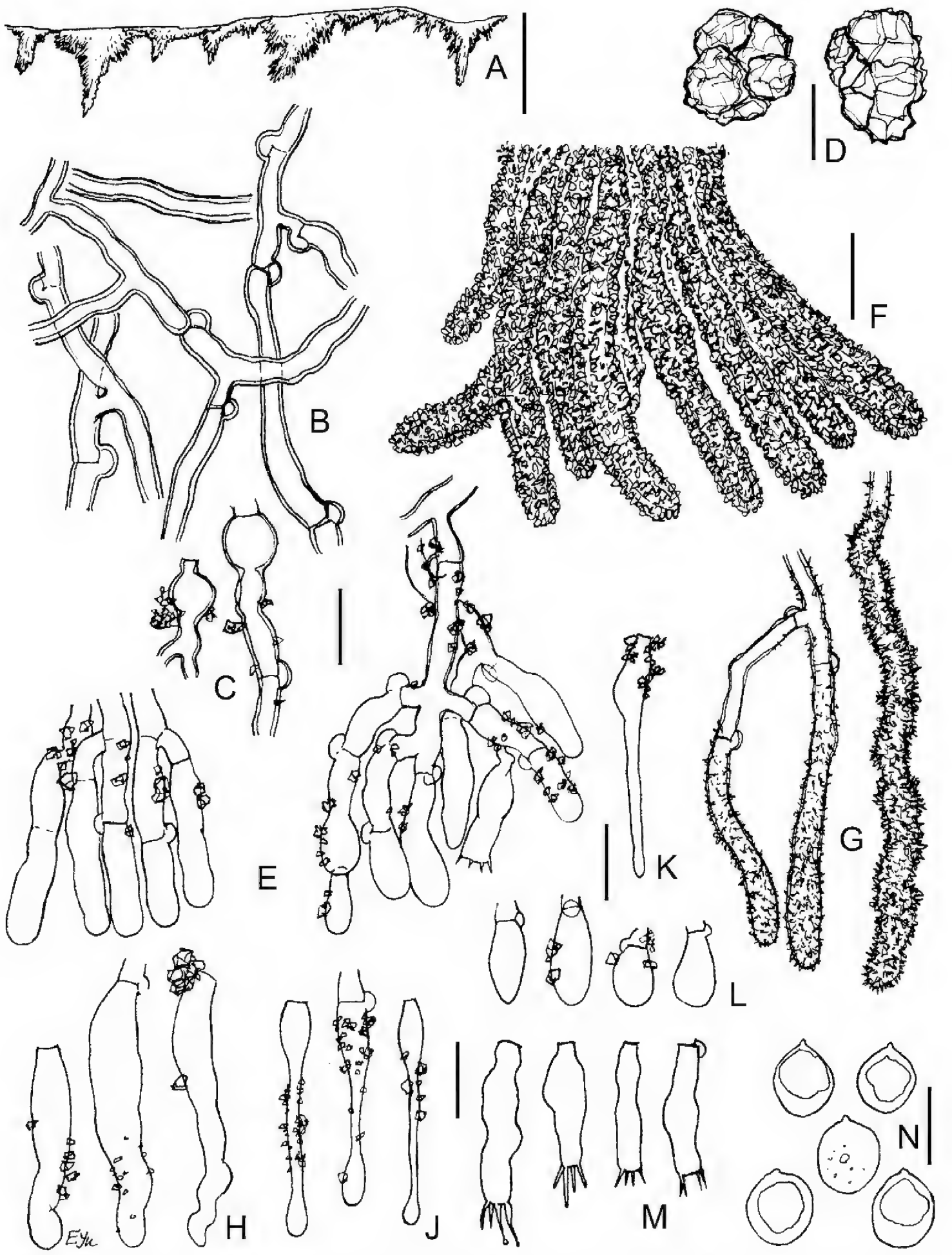

Figure 5. Micromorphology of *Xylodon filicinus* (MSK-F 12369, holotype): **A** vertical section through basidioma **B** subicular hyphae **C** inflations on hyphae in lower subhymenium **D** crystals from subiculum **E** portions of hymenium and subhymenium **F** bundle of encrusted projecting hyphae **G** separate projecting hyphae **H** subcylindrical cystidia **J** capitate cystidia **K** hyphoid cystidium **L** basidioles **M** basidia **N** basidiospores. Scale bars: 100 μm (**A**); 10 μm (**B–M**); 5 μm (**N**).

in clusters 15–18 µm diam. Subhymenial hyphae moderately branched, partly short-celled and slightly inflated, 2–3.5(–4) µm diam., lightly encrusted. Projecting hyphae in aculei richly encrusted, 20–45 × 5–7 µm in encrusted part, with clamped and simple septa, basally thick-walled, then becoming thin-walled, obtuse, sometimes subacute at apex. Cystidia in hymenium thin-walled, lightly encrusted, of three types: (1) subcylindrical, often slightly tapered to apex, numerous, 20–35 × 4.5–5.5 µm; (2) capitate, rare, 26–32 µm long, 3–5 µm wide at base, 2.5–3 µm wide at apex; (3) hyphoid to narrowly ventricose, about 30 × 4.5 µm. Basidioles ellipsoid, ovoid, clavate, 7.5–18 × 4.5–7.5 µm, more or less encrusted. Basidia utriform, (14–)16–20 × (3.5–)4.5–5.5 µm, thin-walled, smooth or sparsely encrusted, with four sterigmata 2–6.5 × 1–1.5 µm. Spores globose to subglobose, 4–5(–5.5) × (3.7–)4–4.5 µm, holotype L = 4.7 µm, W = 4.1 µm, Q = 1.1–1.2, thin-walled, often with one large oil-like globule, negative in Mz, weakly cyanophilous, with minute apiculus.

Distribution and ecology. From the lower mountainous belt in Taiwan, on dead fern rachises.

Etymology. from Latin *filix* – fern, refers to the occurrence on dead fern rachises.

Additional specimen examined. TAIWAN, the same locality and the same substrate as holotype, leg. E. Yurchenko, 31 Jul 2011 (field No. 18; MSK-F 12870; dup. in KAS).

Remarks. The distinctive features of this species are the pruinose, minutely odontioid basidiomata, fascicles of richly encrusted projecting hyphae in aculei and the three types of cystidia. *Xylodon filicinus* is morphologically similar to *X. hyphodontinus*, which differs in having projecting hyphae in the aculei that are straighter with more septa, a denser subhymenium composed of short-celled hyphae, short, ventricose cystidioles and spore walls that are slightly thickened at maturity (see Fig. 6).

Xylodon follis Riebesehl, Yurchenko & Langer, sp. nov.

MycoBank MB827464

Figs 3c, 7

Holotype. REUNION, Forêt Notre Dame de la Paix, Sentier botanique, 21°15.8'S, 55°36.1'E, 1720 m a.s.l., on angiosperm wood, leg. J. Riebesehl, M. Schröder, M.M. Striegel, 12 Mar 2015 (FR-0249814; isotypes in KAS (as L1040) and MSK).

Description. Basidiomata effused, cream-coloured, about 1–5 cm in extent, soft-membranaceous, continuous, finely aculeate, between aculei 50–200 µm thick; aculei narrowly conical or nearly cylindrical, 80–170 × 20–40(–60) µm, 10–12/mm, fragile, slightly fimbriate at apices, sterile. Margin abrupt. Hyphal system monomitic; hyphae clamped and simple septate, colourless, (1–)2–3.5 µm diam. Subiculum little differentiated, composed of thin- to slightly thick-walled hyphae. Hyphae in aculeal trama mostly parallel, thin- to thick-walled (walls up to 1 µm thick), projecting through aculeal apices and loosely encrusted with crystals about 1–3 µm long in KOH. Subhymenium thickening; subhymenial hyphae moderately branched, thin-walled, smooth. Capitate cystidia numerous, projecting and immersed, in subhymenium, hymenium and aculei,

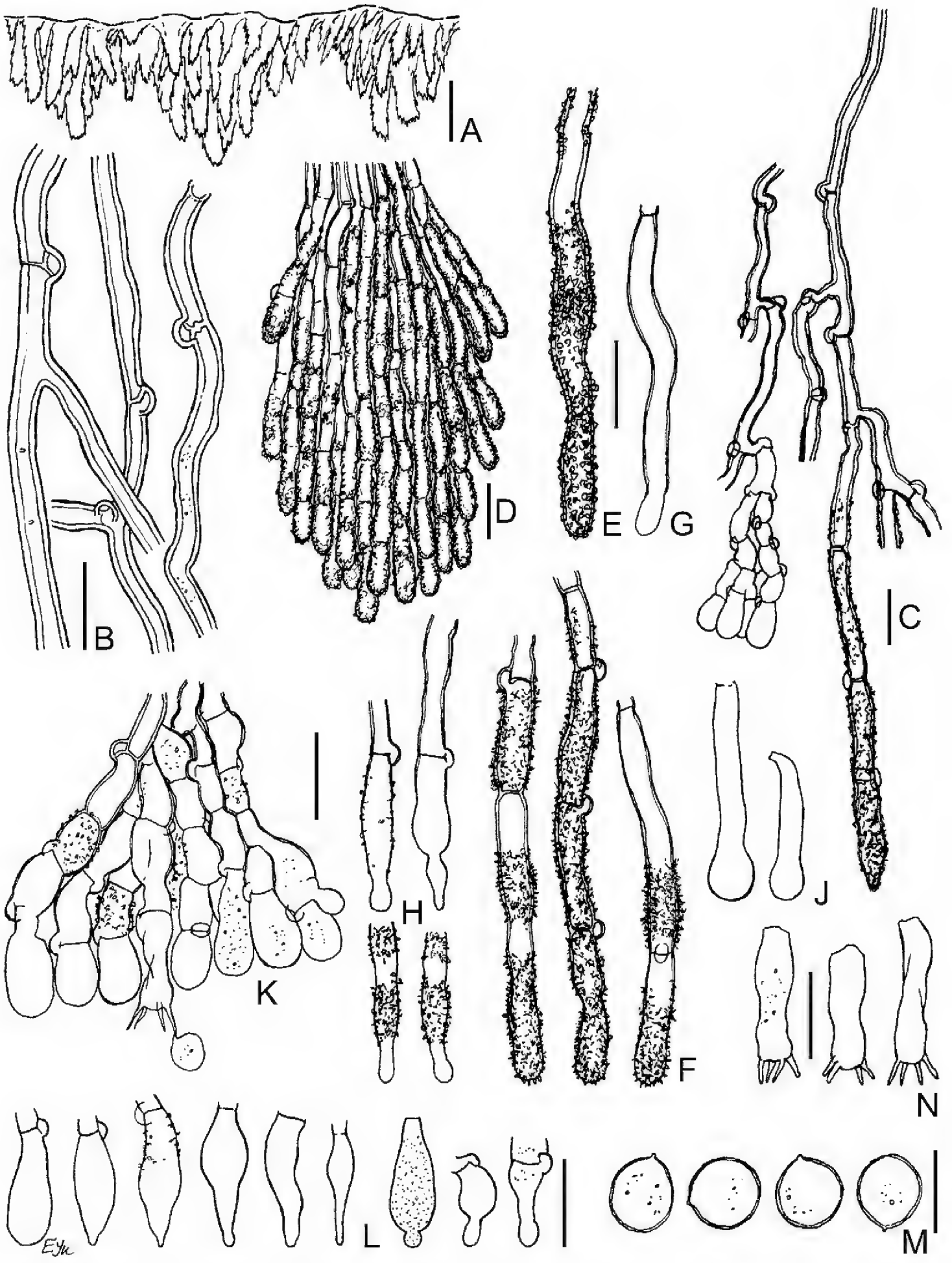

Figure 6. Micromorphology of *Xylodon hyphodontinus*. LIP GG-MAR 15-127: **A** vertical section through basidioma **B** subicular hyphae **C** excerpt of tramal hyphae to hymenium and projecting hyphae **D** bundle of encrusted aculeal hyphae **E** encrustation on projecting hypha in water **F** encrustation on projecting hyphae in 3% KOH **G** naked projecting hyphal end **H** variously shaped hyphal ends **J** capitate cystidia **K** portion of hymenium and subhymenium **L** basidioles and cystidioles **M** basidiospores. LIP GG-MAR 12-238: **N** basidia. Scale bars: 100 μm (**A**); 10 μm (**B–L, N**); 5 μm (**M**).

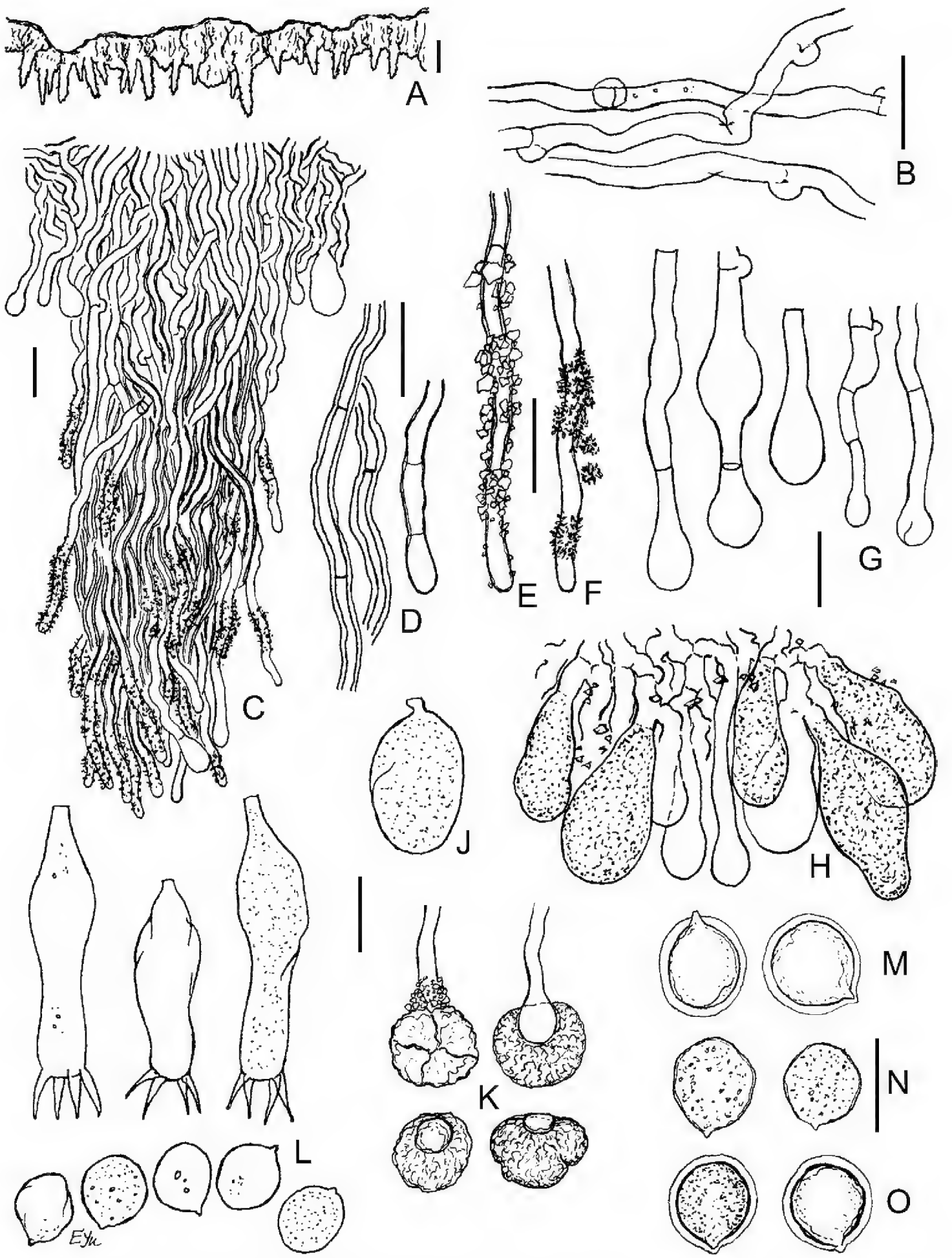

Figure 7. Micromorphology of *Xylodon follis* (FR-0249814, holotype): **A** vertical section through basidioma **B** subicular hyphae **C** vertical section through aculeus **D** lower and apical part of aculeal hyphae with adventitious septa **E** encrusted aculeal hyphae in water **F** partially dissolved crystals on aculeal hyphae in 3% KOH **G** capitate cystidia **H** portion of hymenium **J** vesicular basidiole **K** capitate encrusted cystidia and their detached resinous caps **L** basidia and basidiospores **M** basidiospores in 3% KOH **N** basidiospores in water **O** basidiospores in CBL. Scale bars: 100 µm (**A**); 10 µm (**B–N**).

17–30(–40) × 4.5–9 µm, with 1–2 adventitious septa in stalk, apical cap encased with resinous encrustation 6–12 µm wide, easily dissolving in KOH and Mz, unchanged in CBL. Hyphidial elements common in hymenium, 17–27 × 2.3–3.2 µm. Basidioles pyriform or ellipsoid, 17–28 × 8–12 µm, with granular contents, smooth or slightly encrusted. Basidia utriform or suburniform, thin-walled, smooth, 32–37 × 9–10 µm, with 4 sterigmata 4–6.5 × 1.3–2.3 µm. Spores globose to subglobose, colourless, with homogeneous or granular contents, smooth, inamyloid, indextrinoid, cyanophilous, thin-walled, (7.5–)8–9.5(–10) × 7–8.5 µm, holotype L = 8.6 µm, W = 7.6 µm, Q = 1.0–1.2, outer wall layer sometimes swelling in KOH and CBL, with rounded-triangular apiculus.

Distribution and ecology. The species is so far known from Réunion (Mascarene Archipelago) and inhabits dead wood.

Etymology. from Latin *follis* – bag or bubble, referring to shape of the spores, basidioles and capitate cystidia found in this species.

Additional specimen examined. REUNION, Forêt de Bébour, 1328 m asl., leg. E. Langer, G. Langer, E. Hennen, 20 Mar 1998 (KAS-GEL 4951; dupl. in MSK).

Remarks. This taxon differs from other *Xylodon* species by its unusually large basidia, large globose basidiospores with walls that swell in KOH and CBL and numerous simple septa as well as clamps on the hyphae. The swelling of spore walls was observed in some spores; spores were unaffected in water mounts. The hymenium has a granular appearance visible under 100× magnification because of the resinous cap developed on the capitate cystidia. The resinous caps are observed only in CBL and are easily detaching in squash preparations. Intermediate forms in morphology of hyphidia to capitate cystidia and of capitate cystidia to pyriform basidioles were frequently observed.

Xylodon pseudolanatus **Nakasone, Yurchenko & Riebesehl, sp. nov.**
MycoBank MB827465
Figs 3d, 8

Holotype. BELIZE: Cayo District, Mountain Pine Ridge, on corticated hardwood branch, leg. K.K. Nakasone, 24 Nov 2001 (CFMR FP-150922; isotypes in KAS and MSK; ex-type culture CFMR FP-150922-sp; ex-type ITS sequence MH880220; ex-type 28S sequence MH884909).

Description. Basidiomata effused, membranaceous, cream-coloured, 1–6 cm in extent, odontioid with conical aculei 50–120 µm long and 25–65 µm diam. at base, 8–14 aculei/mm. Subiculum between aculei very loose, minutely porulose, 100–150 µm thick. Margin pale cream-coloured, abrupt or diffuse, up to 2 µm wide. Hyphal system monomitic, hyphae clamped at all primary septa, colourless. Subicular hyphae little branched, mostly thick-walled, 2.5–4 µm diam., smooth or scarcely encrusted. Subhymenial hyphae richly branched, thin-walled, 2–3.5(–4.5) µm diam., smooth or slightly encrusted. Aculei consisting mostly of projecting hyphae. Projecting hyphae moderately flexuous, (3–)3.5–5 µm diam., slightly thick-walled, loosely encrusted, clamped at septa. Capitate cystidial elements found mostly in subhymenium and subiculum,

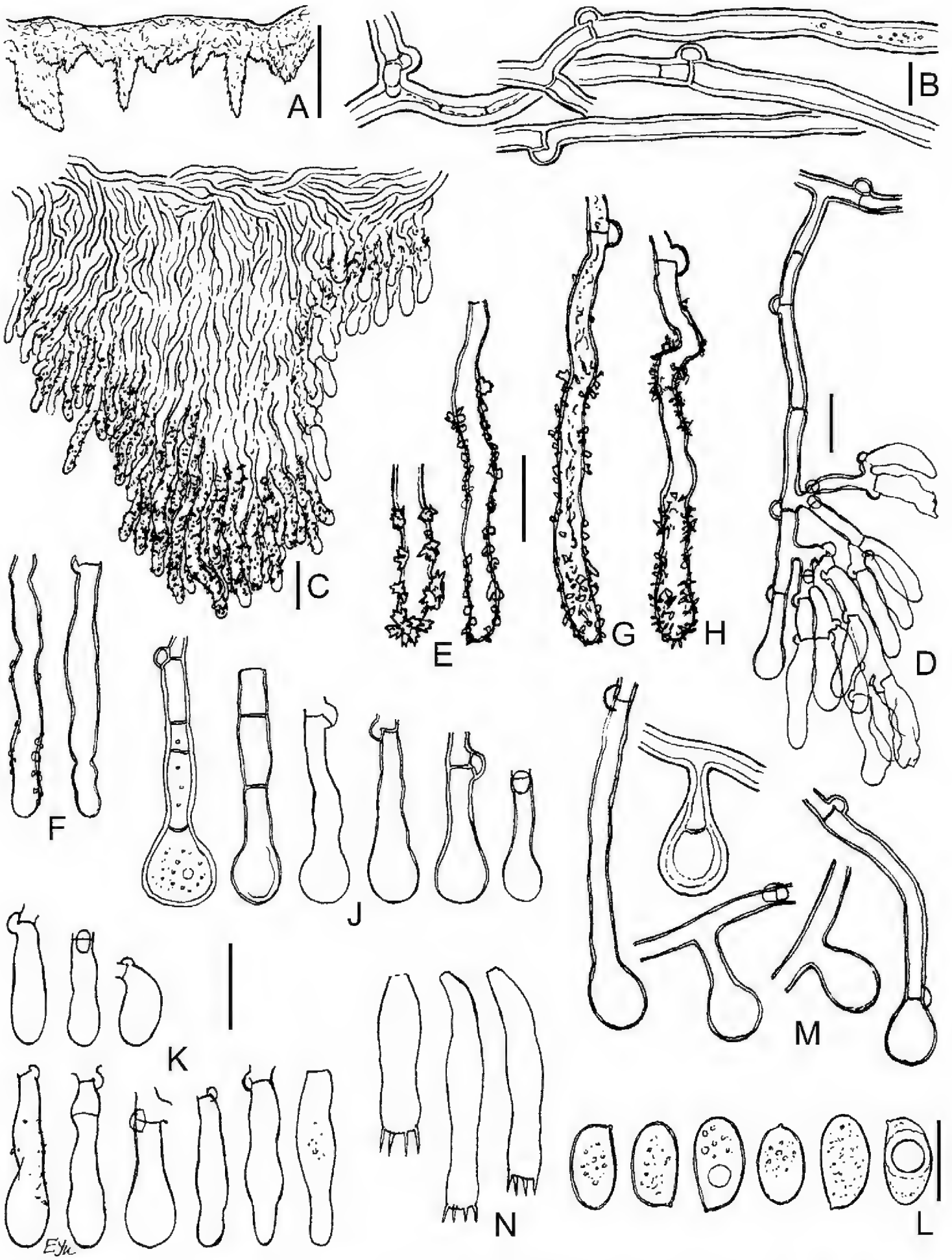

Figure 8. Micromorphology of *Xylodon pseudolanatus*. CFMR: FP-150922 (holotype): **A** vertical section through basidioma **B** subicular hyphae **C** vertical section through aculeus **D** detail of subicular hyphae and hymenium **E, F** projecting aculeal hyphae in 3% KOH **G** projecting aculeal hyphae in water **H** projecting aculeal hyphae in Mz **J** capitate cystidia in hymenium **K** basidioles **L** basidiospores. CFMR: HHB-6925: **M** capitate cystidia in subiculum **N** basidia. Scale bars: 100 µm (**A**); 10 µm (**C–K, M, N**); 5 µm (**B, L**).

scattered to frequent, terminal or lateral, smooth, thin- to thick-walled, aseptate or with adventitious septa, (8–)15–30 × (4.5–)5–6.5(–8.5) µm. Basidioles clavate to subcylindrical, sometimes slightly tapering to apex, 7–22 × 4–5 µm. Basidia cylindrical, sometimes slightly constricted, 16–30 × 4–4.3 µm, thin-walled, smooth, with four sterigmata about 2.5 × 0.2 µm. Spores narrowly ellipsoid to oblong, 5–6(–6.3) × (2.5–)3–3.5 µm, holotype L = 5.5 µm, W = 3.2 µm, Q = 1.7, thin- or slightly thick-walled, colourless, smooth, with minute apiculus, inamyloid, indextrinoid, weakly cyanophilous.

Distribution and ecology. South-eastern USA and Central America, on dead wood of angiosperms.

Etymology. From Greek *pseudo-* – false, refers to its similarity to *X. lanatus*.

Additional specimens examined. USA: Alabama, Escambia County, 3 miles east of Flomaton, on bark of *Taxodium distichum* (L.) Rich. (CFMR FP-103492), on bark of *Quercus* sp. (CFMR FP-103500), leg. A.S. Rhoades, 1 Nov 1952; Florida, Marion County, Okalawaha River, on dead inflorescence of *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult. f., leg. H.H. Burdsall, Jr., 3 Aug 1972 (CFMR HHB-6925; dupl. in KAS and MSK); Louisiana, Baton Rouge, on *Melia azedarach* L., leg. C.J. Humphrey & C.W. Edgerton, 29 Aug 1909 (CFMR FP-5519).

Remarks. The diagnostic features of this species are the minutely odontioid hymenophore, bundles of sparsely to moderately encrusted hyphae, projecting from aculeal apices, embedded capitate cystidia, cylindrical basidia and narrowly ellipsoid basidiospores. Some hymenial elements in this species are intermediate in morphology between basidioles, capitate cystidia and hyphal ends. *Xylodon pseudolanatus* can be distinguished from similar species in the key below (see Discussion).

Xylodon hyphodontinus **(Hjortstam & Ryvarden) Riebesehl, Yurchenko & G.Gruhn, comb. nov.**

MycoBank MB827758

Fig. 6

Odontiopsis hyphodontina Hjortstam & Ryvarden, Mycotaxon 12(1): 180 (1980) (Basionym). Typus of *O. hyphodontina*: TANZANIA, Morogoro Prov., Morogoro distr., Uluguri Mts., Morning Side Res. sta. ca. 5 km S of Morogoro, substrate unknown, leg. L. Ryvarden, 24–26 Feb 1973 (O L. Ryvarden 10949 – holotype).

= *Hydnum ambiguum* Berk. & Broome, Journal of the Linnean Society, Botany 14(73): 60 (1873). Typus of *H. ambiguum*: SRI LANKA, Central Province, on dead wood (Berkeley No. 974 – holotype).

= *Odontiopsis ambigua* (Berk. & Broome) Hjortstam, Mycotaxon 28(1): 35 (1987).

= *Pteridomyces sphaericosporus* Boidin, Lanq. & Gilles, Mycotaxon 16(2): 490 (1983).

Remarks. This new combination is based on the phylogenetic analyses of the ITS and 28S sequences as well as morphological study of specimens, including the holotype of *O. hyphodontina*. Originally, the collections from Martinique and French Guyana were

identified as *O. ambigua*, but the molecular data clearly show that these collections are embedded in *Xylodon* (Figs 1, 2). Although *H. ambiguum* is the oldest name for this taxon, it cannot be transferred to *Xylodon* because the name is preoccupied by *X. ambiguus* (Peck) Kuntze (= *Veluticeps ambigua* (Peck) Hjortstam & Telleria). *Odontiopsis ambigua*, *P. sphaericosporus* and *O. hyphodontina* were recognised as conspecific by Hjortstam (1987, 1991). *Odontiopsis hyphodontina* is the next oldest name and is chosen to represent this taxon. As *O. hyphodontina* is also the type of *Odontiopsis* Hjortstam & Ryvarden, *Odontiopsis* concomitantly becomes a synonym of *Xylodon*.

The newly generated ITS and 28S sequences of *X. hyphodontinus* hold comparable positions in a clade that includes three distinct lineages in both phylogenetic trees (Figs 1, 2). Specimens KAS-GEL9222 from Kenya and LIP GG-GUY13-044 from French Guyana each represent distinct lineages from the third lineage of LIP GG-MAR15-127 and LIP GG-MAR12-238 from Martinique. As species in *Hyphodontia* s.l. can be readily distinguished with ITS or 28S sequences, these three lineages should result in the recognition of three different species. However, we were not able to identify any definite morphological differences amongst the lineages in comparison with the holotype material from Tanzania. Cultures are not available for these specimens, thus intercompatibility tests are not possible. As a result, we decided to treat all three lineages as *X. hyphodontinus* at this time.

Xylodon vesiculosus **Yurchenko, Nakasone & Riebesehl, nom. nov.**
MycoBank MB827759
Figs 3e, 9

Replaced synonym. *Odontia vesiculosa* G. Cunn., Transactions and Proceedings of the Royal Society of New Zealand 86(1): 75 (1959) nom. inval.

Typus. NEW ZEALAND: Otago, Alton Valley, Tuatapere, leg. J.M. Dingley, Feb 1954 (PDD-18112 – holotype).

Cunningham (1959) described this new taxon as *Odontia vesiculosa* G. Cunn. Earlier, *Odontia vesiculosa* Burt was used for another species (Povah 1929). Consequently, *Odontia vesiculosa* G. Cunn. is an illegitimate name and a new name is required for this taxon (see Art. 6.11, 7.4 and 58.1 in Turland et al. 2018).

Below is a description based on the isotype of *X. vesiculosus* (CFMR).

Description. Basidiomata effused, odontioid, membranaceous, with a densely odontioid, ochraceous hymenial surface. Margin mostly abrupt, some parts thinning out. Hymenophoral aculei cylindrical to conical, acute apically, 130–350 µm long, 60–150 µm diam. at base, 4 per mm. Subiculum 100–150 µm thick, minutely cracking. Hyphal system monomitic; hyphae clamped at all primary septa. Subicular and tramal hyphae thick-walled (wall up to 1.5 µm), 2.5–4 µm wide, often with narrow lumen, smooth, colourless, looking faint yellowish in mass due to refractive walls. Subhymenium well developed; hyphae richly branched, thin- to slightly thick-walled, yellowish in mass. Aculei bearing skeletal-like, naked or poorly encrusted, immersed hyphal ends

and variously encrusted, thick-walled, projecting hyphae in bunches, 3.5–5 µm wide. Capitate elements common, as lateral branches on tramal or subhymenial hyphae, (25–)30–55 × 6.5–10.5 µm, thin- to thick-walled, aseptate or with 1–2 adventitious septa. Basidioles clavate, subcylindrical, utriform. Basidia utriform to subcylindrical and clavate, 15–22 × 4–5 µm, thin-walled, smooth, with four sterigmata ca. 2 × 0.5 µm. Spores ellipsoid to narrowly ellipsoid or short cylindric, 5.3–6.3(–7) × 3–4 µm, holotype L = 5.9, W = 3.4, Q = 1.8 (n = 22), with adaxial side flat to convex, smooth, thin-walled, colourless, with minute apiculus, inamyloid, indextrinoid, acyanophilous.

Remarks. This species was considered conspecific with *Xylodon lanatus* from North America (Burdsall and Nakasone 1981, Wu 1990, Gorjón and Greslebin 2012), but we observed significant morphological differences. For example, in *X. vesiculosus*, the basidiomata have a denser, tough-membranaceous texture compared to the soft woolly basidiomata of *X. lanatus*. In addition, the aculei in *X. vesiculosus* are larger and the basidia are thin-walled in contrast to the smaller aculei and basally thick-walled basidia found in *X. lanatus* (compare Figs 9, 10). See Discussion for a key to *X. lanatus*, *X. vesiculosus* and allied taxa.

Xylodon niemelaei **(Sheng H.Wu) Hjortstam & Ryvarden, Synopsis Fungorum 26: 28 (2009)**

≡ *Hyphodontia niemelaei* Sheng H. Wu, Acta Botanica Fennica 142:98 (1990).

Xylodon rhizomorphus **(C.L.Zhao, B.K.Cui & Y.C.Dai) Riebesehl, Yurchenko & Langer, Mycological Progress 16(6): 649 (2017).**

≡ *Hyphodontia rhizomorpha* C.L.Zhao, B.K.Cui & Y.C.Dai, Cryptogamie, Mycologie 35(1):92 (2014).

Xylodon reticulatus **(C.C.Chen & Sheng H.Wu) C.C.Chen & Sheng H.Wu, Mycoscience 59(5): 349 (2018).**

≡ *Hyphodontia reticulata* C.C.Chen & Sheng H.Wu, Mycological Progress 16(5): 558 (2017).

Remarks. Molecular and morphological analyses demonstrate that the three taxa listed above are very similar. The 11 samples of *X. niemelaei*, 3 of *X. rhizomorphus* and 3 of *X. reticulatus* formed a strongly supported clade (99 BS, 1 PP) in the ITS phylogram (Fig. 1). In addition, three samples representing two of the species are found in a strongly supported clade (100 BS, 1 PP) in the 28S tree (Fig. 2), differing in only one position in the associated alignment.

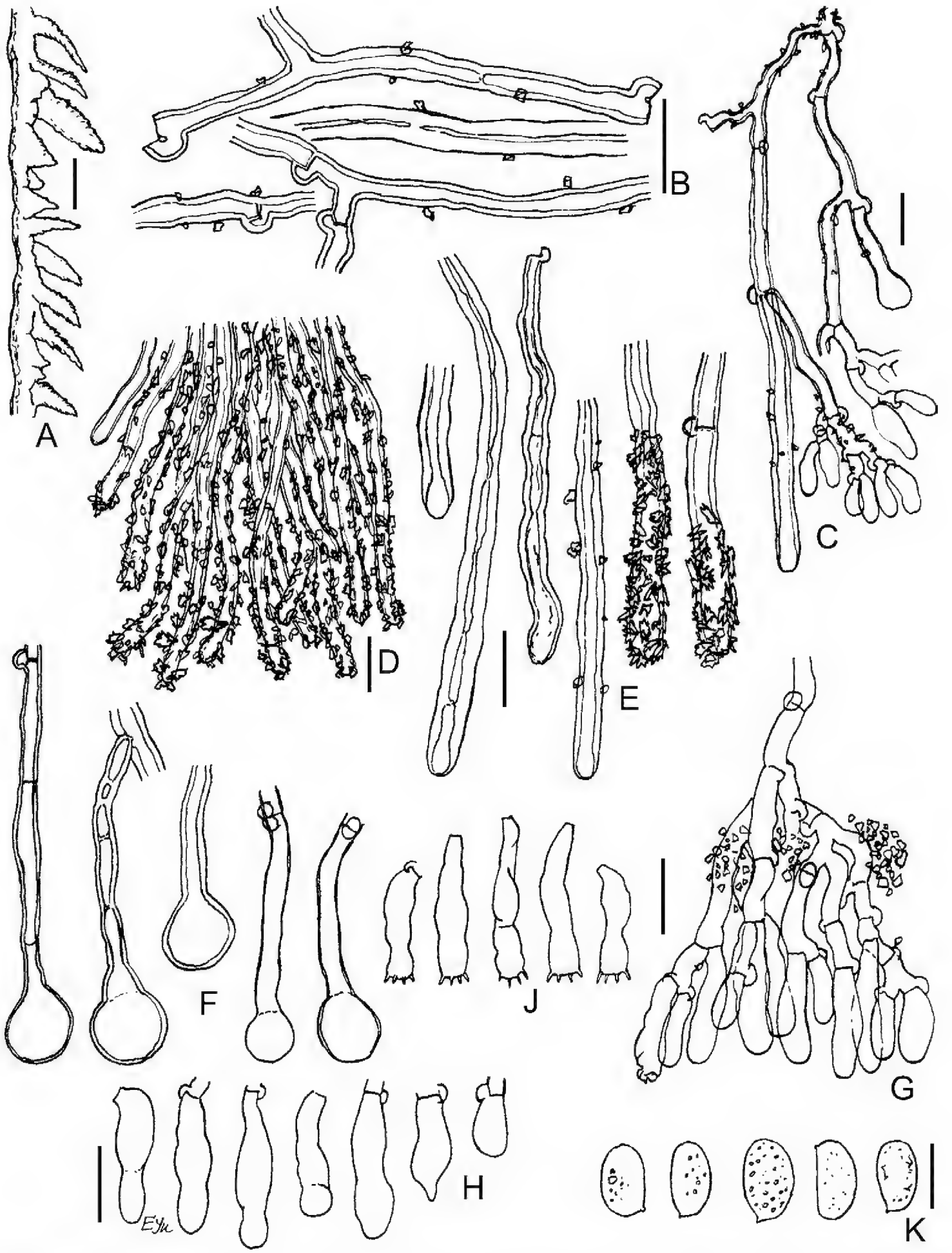

Figure 9. Micromorphology of *Xylodon vesiculosus* (PDD-18112, isotype): **A** vertical section through basidioma **B** subicular hyphae **C** excerpt of tramal hyphae to hymenium and skeletoid hyphae **D** bundle of projecting aculeal hyphae **E** smooth and variously encrusted aculeal hyphae **F** capitate cystidia **G** portion of hymenium and subhymenium **H** basidioles **J** basidia **K** basidiospores. Scale bars: 250 µm (**A**); 10 µm (**B–J**); 5 µm (**K**).

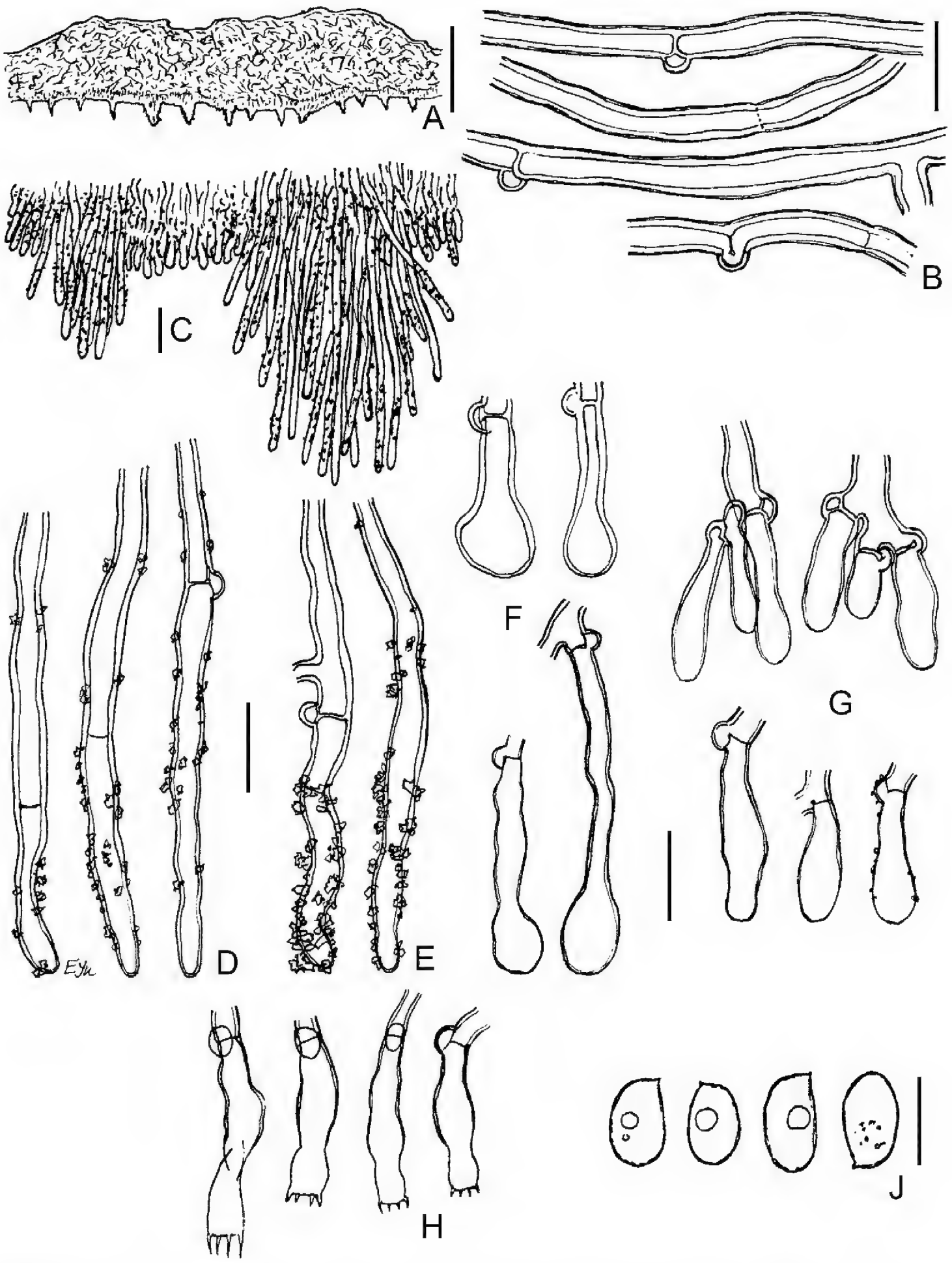

Figure 10. Micromorphology of *Xylodon lanatus* (CFMR: HHB-8925, holotype): **A** vertical section through basidiomata **B** subicular hyphae **C** vertical section through aculei and hymenium **D** projecting hyphae in 3% KOH **E** projecting hyphae in Mz **F** capitate cystidia **G** basidioles **H** basidia **J** basidiospores. Scale bars: 500 μm (**A**); 20 μm (**C**); 10 μm (**B, D–H**); 5 μm (**J**).

Xylodon niemelaei was described and illustrated in detail by Wu (1990) and Langer (1994). It is characterised by a poroid hymenophore, embedded and hymenial capitate cystidia, small, subulate or fusoid hymenial cystidia and encrusted hyphal ends mainly developed at the pore edges but sometimes also in other areas. At the morphological level, the bladder-like embedded cystidia and hyphal encrustations appear identical in *X. niemelaei* (Langer 1994), *X. rhizomorphus* (Zhao et al. 2014) and *X. reticulatus* (Chen et al. 2017). Spore size and spore quotient overlap in these three species. *Xylodon rhizomorphus* occurs in south-western China, whereas *X. reticulatus* occurs in Taiwan and Japan. *Xylodon niemelaei* is reported also from these three countries and furthermore from Réunion, Africa and South America (Langer 1994), but the last two reports require morphological and molecular confirmation.

Specimens examined. *Xylodon niemelaei* – REUNION: Forêt Mare-Longue, on dead stump of angiosperm wood, leg. J. Riebesehl, M. Schröder, M.M. Striegel, 12 Mar 2015 (FR-0249846, dupl. as L1087 in KAS); on lumber, leg. J. Riebesehl, M. Schröder, M.M. Striegel, 12 Mar 2015 (FR-0249174, dupl. as L1077 in KAS); on brown-rotten wood, leg. E. Langer, G. Langer, E. Hennen, 21 Mar 1998 (KAS-GEL 4998); Forêt Notre-Dame de la Paix, on dead wood of *Monimia rotundifolia* Thouars, leg. E. Langer, 11 Mar 2013 (FR-0219860, dupl. as L0002 in KAS); on dead angiosperm wood, leg. J. Riebesehl, M. Schröder, M.M. Striegel, 10 Mar 2015 (FR-0249811, dupl. as L1031 in KAS); on white-rotten wood, leg. E. Langer, G. Langer, E. Hennen, 19 Mar 1998 (KAS-GEL 4904); Le Petit Tampon, on dead wood, leg. J. Riebesehl, M. Schröder, M.M. Striegel, 9 Mar 2015 (FR-0249225, dupl. as L1007 in KAS); Piton Mont Vert, on dead wood, leg. J. Riebesehl, M. Schröder, M.M. Striegel, 18 Mar 2015 (FR-0249178, dupl. as L1172 in KAS); Plaine des Fougères, on dead wood, leg. E. Langer, 12 Sep 2013 (FR-0249744, dupl. as L0698 in KAS); Sentier de Takamaka, on white-rotten wood, leg. J. Riebesehl, M. Schröder, M.M. Striegel, 26 Mar 2015 (FR-0249289, dupl. as L1269 in KAS).

Xylodon spathulatus (Schrad.) Kuntze, Revisio generum plantarum (Leipzig) 3(2):541 (1898)

≡ *Hydnum spathulatum* Schrad., Spicilegium Florae Germanicae: 178, t. 4:3 (1794).
= *Hyphodontia bubalina* Min Wang, Yuan Y.Chen & B.K.Cui, Phytotaxa 309(1):50 (2017).
≡ *Xylodon bubalinus* (Min Wang, Yuan Y.Chen & B.K.Cui) C.C.Chen & Sheng H.Wu, Mycoscience 59:349 (2018).
= *Hyphodontia chinensis* C.C.Chen & Sheng H.Wu, Mycological Progress 16(5): 554 (2017).
≡ *Xylodon chinensis* (C.C.Chen & Sheng H.Wu) C.C.Chen & Sheng H.Wu, Mycoscience 59: 349 (2018).

Remarks. Based on both molecular data and morphology, we place the taxa *X. bubalinus* and *X. chinensis* in synonymy under *X. spathulatus*. In our phylogenetic analysis of ITS sequence data, the recently described *X. bubalinus* (4 collections) and *X. chinensis* (2 collections) from China form a well-supported clade with *X. spathulatus* (4 collections)

from Europe (97 BS, 1 PP) that is sister to *X. apacheriensis* (Fig. 1). Within this clade are several subclades, with very low bootstrap support (<55), thus subspecies or varieties cannot be identified. The 28S rRNA gene analysis also supports conspecificity between *X. chinensis* and *X. spathulatus* (99 BS, 0.65 PP) (Fig. 2). *Xylodon spathulatus* has three main diagnostic features: prominent (1–2 mm tall) aculei of varied shape, numerous apically acute cystidia with 1–4 slight constrictions and capitate cystidia with a resinous cap. It is described and illustrated by Eriksson and Ryvarden (1976) and Langer (1994). Minor morphological variation amongst the three taxa was observed. For example, *X. chinensis* has ventricose cystidia, similar to those in *X. spathulatus*, but they are sometimes septate at the constrictions. Distinctly ventricose cystidia were not observed in *X. bubalinus*, which instead had hyphoid or subulate cystidioles (Wang and Chen 2017, Fig. 2f). Encrusted hyphal ends at apices of the aculei in *X. bubalinus* and *X. chinensis* are typical of those in *X. spathulatus*. Resinous caps enclosing capitate elements are often absent as in the case of *X. bubalinus*, *X. chinensis*, *X. spathulatus* KAS-GEL2690 (from Germany) and *X. spathulatus* MSK-F 12931 (from Russia). Spore shape and size are similar amongst the three taxa and the spore quotient 1.3–1.4(–1.5) overlaps (Eriksson and Ryvarden 1976, Wang and Chen 2017, Chen et al. 2017). A few spores in *X. chinensis* were up to 6 × 5 µm and may be due to better climatic conditions. The description of *X. spathulatus* is modified to include variable aculei from conical and subulate to distinctly spathuliform and the variable presence of cystidia with resinous caps, mucronate apices and a submoniliform type that are aseptate with more or less blunt apices. Thus *X. spathulatus* is a highly variable but distinctive species that is widely distributed from northern Europe (Eriksson and Ryvarden 1976) to southern China (Chen et al. 2017) and has a preference for old-growth forests (Dvořák et al. 2017). Reports of *X. spathulatus* from North and South America (Ginns and Lefebvre 1993, Hjortstam and Ryvarden 2007b) should be confirmed by molecular sequence data.

Specimens examined. *Xylodon spathulatus* – CZECH REPUBLIC: Zofinsky National Park, on dead deciduous wood, leg. M.M. Striegel, 16 Sep 2015 (KAS-MMS 7224); GERMANY: Baden-Wurttemberg, Bad Waldsee, on dead wood of *Picea abies* (L.) H.Karst., leg. E. Langer, G. Langer, 15 Oct 1992 (KAS-GEL 2690); SWEDEN: Gästrikland, Island Torrö, on dead wood of *Betula* sp., leg. K.H. Larsson, 29 Sep 1988 (GB KHL 7085, dupl. in KAS); RUSSIA: Udmurtia, near Izhevsk town, on *Sorbus aucuparia* L., leg. V.I. Kapitonov, 7 Aug 2012 (MSK-F 12931).

***Xylodon cystidiatus* (A.David & Rajchenb.) Riebesehl & Langer, Mycological Progress 16(6):645 (2017)**

≡ *Schizopora cystidiata* A. David & Rajchenb., Mycotaxon 45:140 (1992).

Remarks. We undertook a thorough morphological analysis of the specimen FR-0249200 (Réunion, Plaine des Fougères, on fallen angiosperm twig, leg. E. Langer, 12 Sep 2013), because it provided the first sequences of *X. cystidiatus*. We are confident that FR-0249200 is *X. cystidiatus*, although we detected minor differences from the

Figure 11. Basidioma of *Xylodon cystidiatus* (FR-0249200). Scale bar: 1 cm.

descriptions in David and Rajchenberg (1992) and Langer (1994). Some of the differences we noticed include: (1) the encrusted cystidia in FR-0249200 are mostly thin-walled with finer crystals; (2) the spores in our specimen were slightly broader 5–6 × 3.5–4.3 µm (L = 5.4 µm, W = 3.9 µm, Q = 1.4) than in published records 5–6 × 3–4 µm. Photographs of the basidioma (Fig. 11) and drawings of the microscopic features (Fig. 12) of FR-0249200 are provided for future identifications.

Discussion

We recognise 77 species of *Xylodon* based on studies by Riebesehl and Langer (2017), Chen et al. (2017, 2018), Kan et al. (2017), Wang and Chen (2017) and results herein (Table 1). Our phylogenetic analyses included 122 ITS and 28S sequences representing 37 *Xylodon* species. The other 40 accepted species in *Xylodon* are based on morphological studies.

In the following discussion, we highlight some of the significant results.

Odontiopsis is a synonym of *Xylodon*

The monotypic *Odontiopsis* Hjortstam & Ryvarden was described in 1980 based on *O. hyphodontina* from Tanzania. Hjortstam (1987) transferred *Hydnum ambiguum* to *Odontiopsis* and placed *O. hyphodontina* in synonymy. Later, *Pteridomyces sphaericosporus* was placed in synonymy with *O. ambigua* by Hjortstam (1991). Analyses of ITS and 28S sequences placed specimens originally identified as *O. ambigua* in the *Xylodon* lineage. Due to nomenclature rules to choose the earliest possible epithet to represent a taxon (see Art. 11.4 in Turland et al. 2018), the name for this taxon is *Xylodon hyphodontinus* and *Odontiopsis* is reduced to a synonym of *Xylodon*.

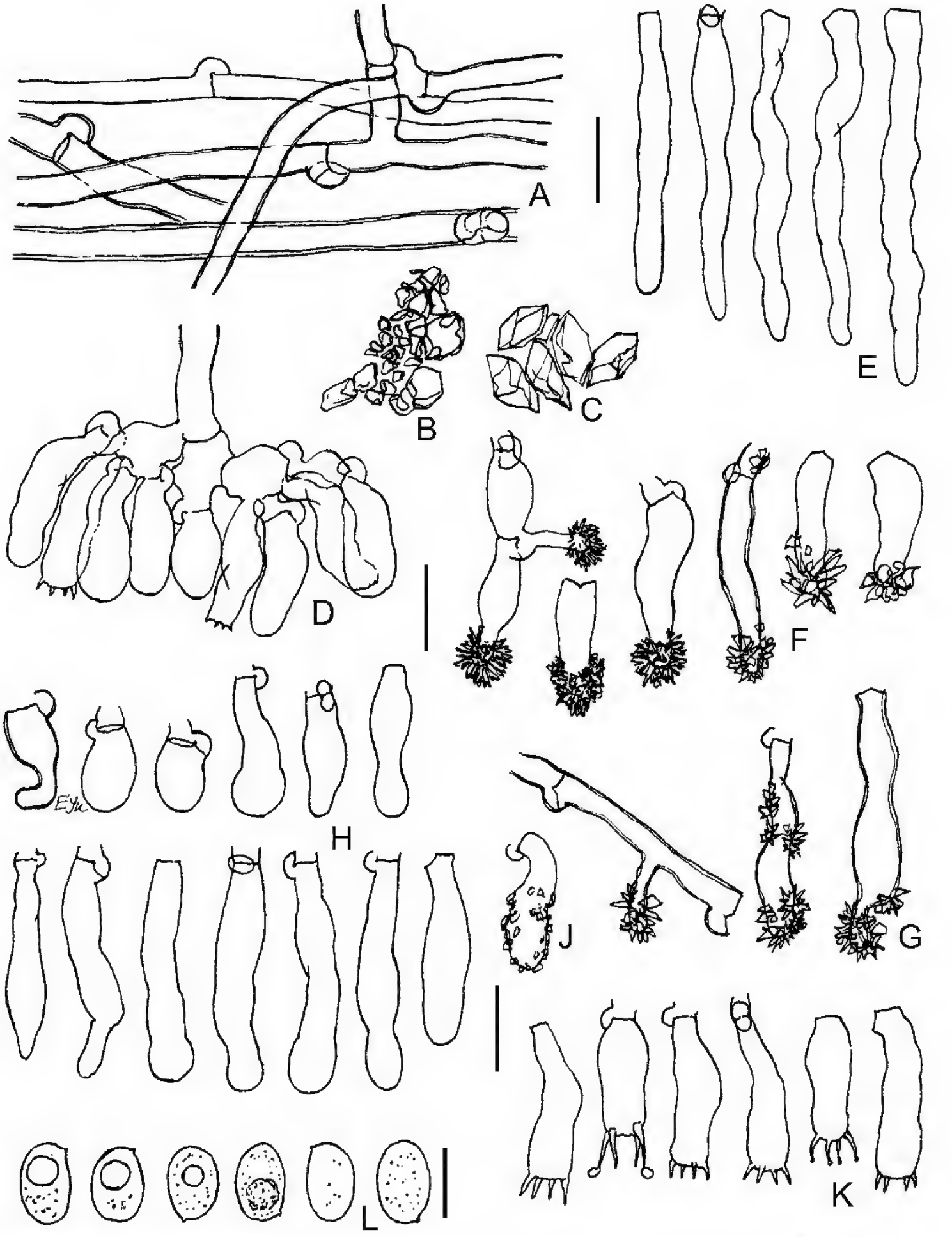

Figure 12. Micromorphology of *Xylodon cystidiatus* (FR-0249200): **A** subicular hyphae **B** crystals from dissepiment in 3% KOH **C** crystals from dissepiment in Mz **D** portion of hymenium and subhymenium **E** hyphal endings from dissepiment edges **F** encrusted cystidia in 3% KOH **G** encrusted cystidia in Mz **H** smooth basidioles and cystidioles **J** encrusted basidiole (in Mz) **K** basidia **L** basidiospores. Scale bars: 10 µm (**A–K**); 5 µm (**L**).

Palifer is a synonym of *Xylodon*

Species in *Palifer* have apically encrusted cystidia that are characteristic of the genus and distinctly different from the lagenocystidia of *Hyphodontia* s.s. (Hjortstam and Ryvarden 2009, Riebesehl and Langer 2017). *Palifer* is defined primarily by morphology because there is only a single ITS sequence available. Phylogenetic studies place *P. verecundus* amongst the *Xylodon* species (Larsson et al. 2006, Fig. 1). The recently described *X. mollissimus* has cystidia that are similar to those of *Palifer* species and ITS sequence analyses place it in a clade with *Xylodon* sp. 1 (Kan et al. 2017, Fig. 1). Although not closely related, *X. mollissimus* and *P. verecundus* are embedded within *Xylodon* and demonstrate that the distinctive cystidia developed in *Palifer* is not a phylogenetically significant character. Thus, we reduce *Palifer* to a synonym of *Xylodon* and propose the following transfers:

Xylodon erikssonii **(M.Galán & J.E.Wright) Riebesehl & Langer, comb. nov.**
MycoBank MB827760

Grandinia erikssonii M.Galán & J.E.Wright, in Galán, Lopez & Wright, Darwiniana 32(1–4):251 (1993) (Basionym).
≡ *Hyphodontia erikssonii* (M.Galán & J.E.Wright) Hjortstam & Ryvarden, Synopsis Fungorum 20: 63 (2005).
≡ *Palifer erikssonii* (M.Galán & J.E.Wright) Riebesehl, Yurchenko & Langer, in Riebesehl & Langer, Mycological Progress 16(6): 646 (2017).

Typus. ARGENTINA, Prov. Bonariae, Videla Dorna, on *Salix babylonica* L., May 1972, Deschamps et al. (BAFC 31920 – holotype).

Xylodon gamundiae **(Gresl. & Rajchenb.) Riebesehl & Langer, comb. nov.**
MycoBank MB827761

Hyphodontia gamundiae Gresl. & Rajchenb., Mycologia 92(6):1159 (2000) (Basionym).
≡ *Palifer gamundiae* (Gresl. & Rajchenb.) Hjortstam & Ryvarden, Synopsis Fungorum 22: 9 (2007).

Typus. ARGENTINA, Tierra del Fuego, Dpto. Ushuaia, Estancia El Valdéz, on *Nothofagus pumilio* (Poepp. & Endl.) Krasser, 4–5 Mar 1996, A. Greslebin (BAFC 50036 – holotype).

Xylodon hjortstamii **(Gresl. & Rajchenb.) Riebesehl & Langer, comb. nov.**
MycoBank MB827762

Hyphodontia hjortstamii Gresl. & Rajchenb., Mycologia 92(6):1160 (2000) (Basionym).

≡ *Palifer hjortstamii* (Gresl. & Rajchenb.) Hjortstam & Ryvarden, Synopsis Fungorum 22: 9 (2007).

Typus. ARGENTINA, Tierra del Fuego, Parque Nacional Tierra del Fuego, Río Pipo, on *Nothofagus* sp., 7 Nov 1998, A. Greslebin (BAFC 50037 – holotype).

***Xylodon septocystidiatus* (H.X.Xiong, Y.C.Dai & Sheng H.Wu) Riebesehl & Langer, comb. nov.**
MycoBank MB827764

Hyphodontia septocystidiata H.X.Xiong, Y.C. Dai & Sheng H.Wu, Mycologia 102(4):918 (2010) (Basionym).
≡ *Palifer septocystidiatus* (H.X.Xiong, Y.C.Dai & Sheng H.Wu) Riebesehl, Yurchenko & Langer, in Riebesehl & Langer, Mycological Progress 16(6): 649 (2017).

Typus. TAIWAN, Taipei, Kungliao, on rotten angiosperm branch, 25 Nov 1990, Y.F. Lin (TNM Lin 90202 – holotype).

***Xylodon verecundus* (G.Cunn.) Yurchenko & Riebesehl, comb. nov.**
MycoBank MB827765

Peniophora verecunda G.Cunn., Transactions and Proceedings of the Royal Society of New Zealand 83(2):262 (1955) (Basionym).
≡ *Palifer verecundus* (G.Cunn.) Stalpers & B.K.Buchanan, New Zealand Journal of Botany 29(3): 339 (1991).
≡ *Hyphodontia verecunda* (G.Cunn.) Hjortstam & Ryvarden, Mycotaxon 64: 237 (1997).

Typus. NEW ZEALAND, Auckland, Hauhangaroa Range, Taupo, on decayed decorticated wood of *Dacrydium cupessinum* Sol., Mar 1953, J.M. Dingley (PDD 12513 – holotype).

Notes

The three species *Palifer rickii* (Hjortstam & Ryvarden) Riebesehl, Yurchenko & Langer, *P. seychellensis* Dämmrich & Rödel and *P. wrightii* (Hjortstam & Ryvarden) Hjortstam & Ryvarden are today already accepted in other genera as *Xylodon rickii* (Hjortstam & Ryvarden) K.H. Larss. (Viner et al. 2018), *Sceptrulum inflatum* (Burt) K.H. Larss. (Larsson 2014) and *Hyphodontia wrightii* Hjortstam & Ryvarden (Gorjón 2012).

Xylodon lanatus and allied species

Xylodon lanatus was originally described by Burdsall and Nakasone (1981) based on collections from North America and New Zealand. A comparative morphological study of specimens, annotated as *X. lanatus* from Taiwan and North America, revealed that *X. lanatus* is a complex of morphologically similar species. The New Zealand specimen, *X. vesiculosus*, was discussed above and is considered to be a distinct species. The specimen *X. lanatus* (TUB-FO 40734) from Taiwan, depicted in Langer (1994), is *X. exilis*. The specimen of *X. lanatus* cited by Hjortstam and Ryvarden (1984) from Nepal is also *X. exilis*. In the protologue of *X. lanatus* (Burdsall and Nakasone 1981), the authors illustrated the paratype (HHB-6925 from Florida, U.S.A.) which is correctly identified as *X. pseudolanatus*. Hjortstam and Bononi (1987) reported *X. lanatus* from Brazil while noting the controversial taxonomic position of this species.

We accept *X. lanatus*, based on the type (CFMR HHB-8925; Figs 3f, 10) and paratype (CFMR HHB-4305), as a distinct species but with a restricted concept. We retain the same diagnostic features, noted in the protologue (basidiomata with well-developed woolly subiculum, terminal vesicular structures on subicular hyphae, poorly differentiated subhymenium, encrusted thick-walled hyphae in tooth apices and capitate cystidia) and add that walls of basidia and subhymenial hyphae directly under hymenial elements are slightly but distinctly thickened. The illustration of *Xylodon lanatus* from Taiwan, provided by Wu (1990), also shows basidia with walls thickened below, but hyphal pegs appear different from *X. lanatus* s.s. We have also determined that *X. echinatus* (Yurchenko et al. 2013) is the most morphologically similar species to *X. lanatus* s.s. A key to the taxa in the *X. lanatus* group is presented here.

1 Basidioma between aculei 0.3–0.5 mm thick, woolly; subhymenial hyphae somewhat thick-walled directly under hymenium **2**

– Basidioma between aculei 0.05–0.15 mm thick, membranaceous or subceraceous; subhymenial hyphae thin-walled **3**

2 Capitate cystidia present; basidia with slightly thickened walls in lower ½–2/3; spores 3–3.5 µm broad, Q = 1.8–2 ..... ***X. lanatus***

– Capitate cystidia absent; basidia thin-walled; spores 3.5–4(–5) µm broad, Q = 1.6–1.9 ..... ***X. echinatus***

3 Subicular hyphae strongly thick-walled (up to 1.5 µm thick), often with narrow lumen; hymenophoral aculei 0.13–0.35 mm long, 4 per mm ..... ***X. vesiculosus***

– Subicular hyphae moderately thick-walled (up to 1–1.2 µm thick), with wide lumen; hymenophoral aculei 0.03–0.12 mm long, 8–14 per mm **4**

4 Projecting hyphae in aculei strongly flexuous, thick-walled (up to 1–1.5 µm thick) in middle and lower part, provided with closely arranged simple and clamped septa, constricted at septa ..... ***X. exilis***

– Projecting hyphae in aculei slightly flexuous, slightly thick-walled, with remote septa, not constricted at septa ..... ***X. pseudolanatus***

Xylodon niemelaei, *X. reticulatus* and *X. rhizomorphus* are very closely related

Phylogenetic analyses of ITS sequences of 17 samples, including 8 new sequences of *X. niemelaei* and 28S sequences of three samples, demonstrate that the three taxa are very similar (Figs 1, 2). ITS sequences from holotypes of *X. reticulatus* and *X. rhizomorphus* were included in the analyses (Fig. 1). The ITS sequences were 98.2–99% similar amongst the taxa, differing at 6–11 sites. Minor morphological differences were noted amongst the taxa. We keep the taxa *X. niemelaei*, *X. reticulatus* and *X. rhizomorphus* as separate species following the results of phylogenetic studies of Chen et al. (2017) and Fernández-López et al. (2018a). The last work was published shortly before the completion of our study and therefore could not be considered further.

However, in our reconstruction, the phylogenetic distances between these taxa are very short, and comparable to those between the OTUs of *X. spathulatus*. Taking into account that these three taxa remain as monophyletic branches, we suppose that they can be subspecies or varieties of one species.

Xylodon bubalinus, *X. chinensis* and *X. spathulatus* are conspecific

Phylogenetic analyses of ITS sequences of 10 samples, including sequences from holotypes of *Xylodon bubalinus* and *X. chinensis* and 28S sequences of *X. spathulatus* and holotype of *X. chinensis* show that the three taxa are conspecific (Figs 1, 2). Amongst the taxa, ITS sequences were 98.7–99.8% similar, differing at up to 8 sites. The hymenophore is quite variable in this group and the presence of the different types of cystidia is also variable. The correct name for this group is *X. spathulatus* with *X. bubalinus* and *X. chinensis* reduced to synonyms.

The classification of *Xylodon australis* in *Xylodon* is confirmed

Xylodon australis is sequenced for the first time and shown in the 28S phylogenetic tree (Fig. 2) and its placement in *Xylodon* is confirmed. The sequenced specimen is from Argentina and was studied by Greslebin et al. (2000). They reported differences in spore morphology in specimens from Argentina, Australia and New Zealand. A molecular study may be able to resolve this species complex.

The paratype material of *Xylodon dimiticus* may be an independent species

Chen et al. (2017) showed that the holotype material of *Xylodon dimiticus* (Jia J.Chen & L.W.Zhou) Riebesehl & Langer Dai 11686 is conspecific with *X. nongravis*. In addition, they also proposed that the paratype material Dai 15321 may be an independent species as shown in the phylograms. We support this view and included Dai 15321 in our phylo-

grams as *Xylodon* sp. 1. The NCBI BLAST search of the ITS sequence of Dai 15321 shows an identity of 93% with the *X. dimiticus* holotype material Dai 11686 as well as with sequences of *X. nongravis*. Although this low similarity value indicates that Dai 15321 is a different species, a further study is needed to identify morphological differences.

Additions to the distribution and morphology of *Xylodon serpentiformis*

A BLAST search of the newly generated *Xylodon serpentiformis* ITS sequences revealed that they are 99% identical to a sequence from South Korea identified as *Hyphodontia* sp. (KUC20121019-31, Jang et al. 2016). *Xylodon serpentiformis* is known from Taiwan and the Canary Islands (Langer 1994). Based on the small distance between Taiwan and South Korea and the similarities of the sequences, the distribution of *X. serpentiformis* is expanded to include South Korea. Langer (1994) cited a specimen of *X. serpentiformis* from the Canary Islands, but this material needs molecular confirmation. A distinctive feature, described for this species, was the presence of flexuous, thick-walled tubular tramacystidia in the aculei (Langer 1994). After our morphological analysis of the holotype of *Hyphodontia serpentiformis* Langer (TUB-FO 40677) and three more specimens (TUB-FO 40675, TUB-FO 40985, TUB-FO 42688), we emend the diagnosis of *X. serpentiformis* as follows: aculei consisting mostly of flexuous, agglutinated projecting hyphae, hyphae slightly thickened or moderately thick-walled at base, then thinning toward apex and partly collapsing at maturity; spores broadly ellipsoid, ellipsoid, subovoid, sometimes narrowly ellipsoid.

Sequences of *Xylodon raduloides* form two subclades in phylogenetic trees

The two subclades of *Xylodon raduloides* in the ITS phylogeny (Fig. 1) appear also in the 28S phylogram (Fig. 2), although with the inclusion of the sister species *X. subtropicus*. Both subclades include specimens from Germany and Australia. Micromorphological distinctions between the clades were not observed, but we noted that, in one of the clades (KAS-JR 02, 03, 09, 26), the hymenophore is pale cream to cream whereas, in the second clade (KAS-JR10, LR 18813), it is yellow-brownish (Fig. 13). Nevertheless, the morphological as well as sequence-based differences are not sufficient to recognise two separate species.

Sequences of *Xylodon flaviporus* form two subclades in phylogenetic trees

In the ITS phylogram, two subclades are also present in the *Xylodon flaviporus* lineage (Fig. 1). Subclade 1 (FR-0249797, KAS-GEL 5047) comprises specimens from Réunion whereas subclade 2 (FCUG 1053, KAS-GEL 3462) comprises specimens from Romania and Taiwan. All other ITS sequences of *X. flaviporus* from the NCBI GenBank are from the northern hemisphere (Romania, South Korea, Taiwan, Turkey and USA) and clustered together in subclade 2 (data in Fig. 1 are reduced to specimens

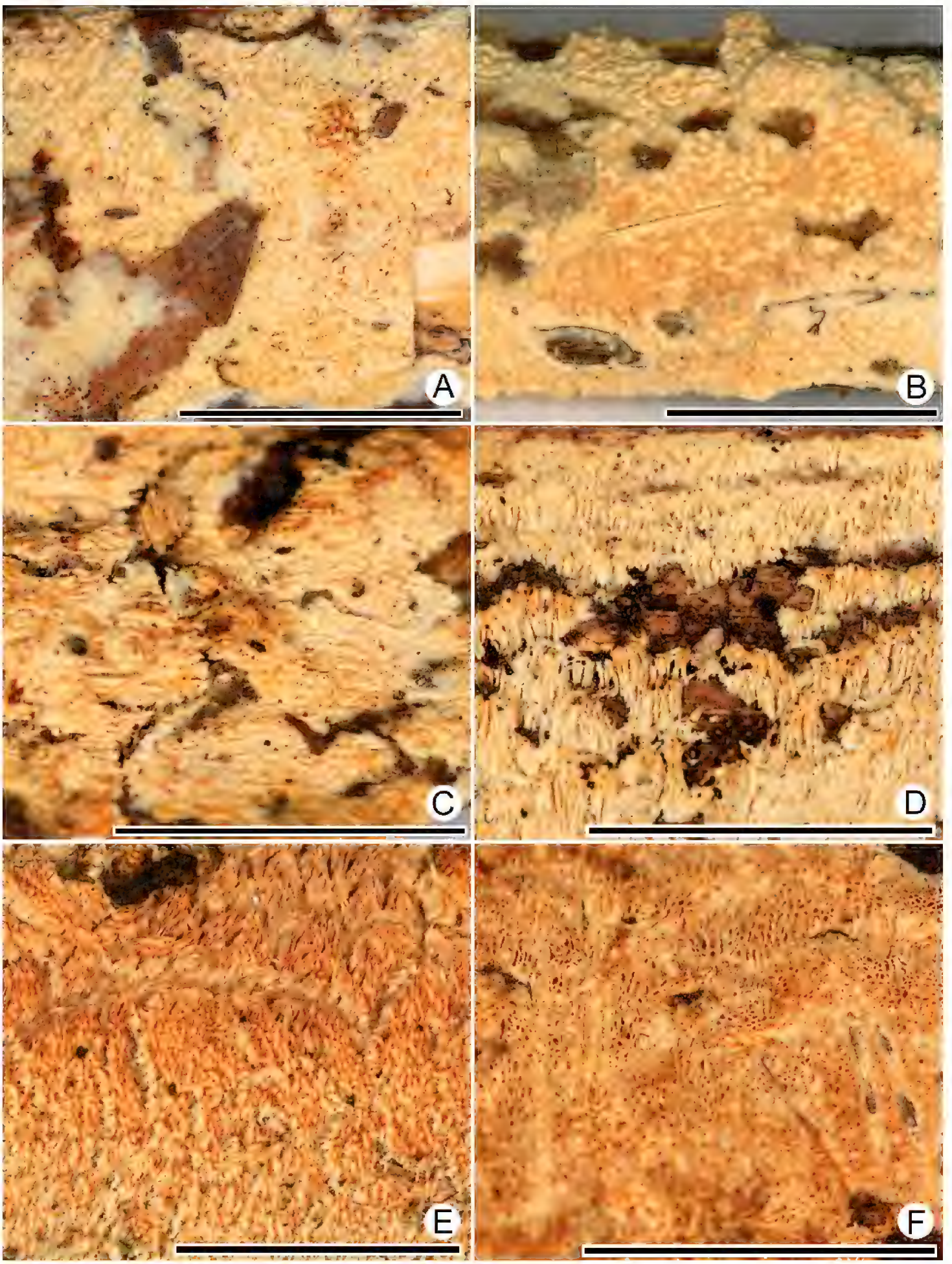

Figure 13. Hymenophores of *X. raduloides*. **A** KAS-JR 02, Germany **B** KAS-JR 03, Germany **C** KAS-JR 09, Germany **D** KAS-JR 26, Germany **E** KAS-JR 10, Germany **F** LR18813, Australia. Scale bars: 1 cm.

from Romania and Taiwan). We did not find micromorphological differences between specimens of the two subclades and the variation in the ITS sequences is too small to merit recognition of two different species.

Xylodon ramicida and *X. quercinus*

Xylodon ramicida and *X. quercinus* are morphologically similar (Ariyawansa et al. 2015), exhibiting slight differences in spore width and shape and different substrate preferences. Their ITS sequences are 98.8–99% similar, differing at just 6–7 positions (*X. quercinus*: Miettinen 15050 and *X. ramicida*: Spirin 7664). Taking into account the similarity values of other *Xylodon* species (*X. spathulatus* 98.7–99%, *X niemelaei* 98.2–99%) and small morphological differences between *X. ramicida* and *X. quercinus*, we believe that *X. ramicida* is a well-defined subspecies within *X. quercinus*. More sequences from both taxa are required, however, before the taxonomic status of *X. ramicida* can be clarified.

The taxonomic status of *Xylodon detriticus*

In this study, we accept *Hyphodontia detritica* (Bourdot) J. Erikss. in *Xylodon* as *X. detriticus*. This combination was introduced by Ţura et al. (2011), recognised as invalid in MycoBank (Art. 36.1a and b, Melbourne Code) and supported in the work by Rosenthal et al. (2017). The first sequenced specimen of this species was GB Nilsson 990902 (Larsson 2007). We have studied this specimen and it is identical to the concept of *Hypochnicium detriticum* (Bourdot) J. Erikss. & Ryvarden (Eriksson and Ryvarden 1976). The alignment between GB Nilsson 990902 and *X. detriticus* UC2023108 (Rosenthal et al. 2017) in ITS2 (ITS1 is unavailable for the previous specimen) showed nearly 100% similarity. We discovered that the ITS2 sequences between *Lagarobasidium detriticum* MA-Fungi 5758 (Dueñas et al. 2009) and GB Nilsson 990902 were 62% identical. Consequently, the taxonomic identity of *Lagarobasidium detriticum* MA-Fungi 5758 needs to be investigated. Viner et al. (2018) came to the same conclusion, but we could not integrate their further results, because this study was already finished when the work of Viner et al. was published.

Conclusion

The usefulness of ITS sequences alone in defining and identifying species in *Xylodon* is approaching its limits. Further studies in *Xylodon* will require sequences from additional genetic markers with more variation. Fernández-López et al. (2018b) published the first phylogenetic tree for *Xylodon* with rpb2 sequences, but it contains only sequences of six different species. Nevertheless, the topology is very similar to our ITS and 28S trees.

Morphological features for defining species in *Xylodon* is also limited. Species, such as *X. spathulatus* with its variability in aculei morphology and in cystidia occurrence and shape, present challenges for identification. In other cases such as *X. hyphodontinus*, ITS sequence differences are significant whereas morphological differences are elusive.

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References

Ariyawansa HA, Hyde KD, Jayasiri SC, Buyck B, Chethana KT, Dai DQ, Dai YC, Daranagama DA, Jayawardena RS, Lücking R, Ghobad-Nejhad M (2015) Fungal diversity notes 111–252– taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 7(1): 27–274. https://doi.org/10.1007/s13225-015-0346-5

Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Ostell J, Pruitt KD, Sayers EW (2018) GenBank. Nucleic Acids Research 46(D1): D41–D47. https://doi.org/10.1093/nar/gkx1094

Boidin J, Gilles G (2003) Homobasidiomycétes Aphyllophorales non porés à basides dominantes à 2(3) stérigmates. Bulletin Trimestriel de la Societe Mycologique de France 119(1–2): 1–17.

Bunyard BA, Chaichuchote S, Nicholson MS, Royse DJ (1996) Ribosomal DNA analysis for resolution of genotypic classes of *Pleurotus*. Mycological Research 100(2): 143–150. https://doi.org/10.1016/S0953-7562(96)80112-2

Burdsall HH, Nakasone KK (1981) New or little known lignicolous Aphyllophorales (Basidiomycotina) from southeastern United States. Mycologia 73: 454–476. https://doi.org/10.1007/s13225-015-0346-5

Chen CC, Wu SH, Chen CY (2017) Three new species of *Hyphodontia* s.l. (Basidiomycota) with poroid or raduloid hymenophore. Mycological Progress 16(5): 553–564. https://doi.org/10.1007/s11557-017-1286-0

Chen CC, Wu SH, Chen CY (2018) *Xylodon subflaviporus* sp. nov. (Hymenochaetales, Basidiomycota) from East Asia. Mycoscience 59(5): 343–352. https://doi.org/10.1016/j.myc.2017.12.004

Chen JJ, Zhou LW, Ji XH, Zhao CL (2016) *Hyphodontia dimitica* and *H. subefibulata* spp. nov. (Schizoporaceae, Hymenochaetales) from southern China based on morphological and molecular characters. Phytotaxa 269(1): 1–13. https://doi.org/10.11646/phytotaxa.269.1.1

Cunningham GH (1959) Hydnaceae of New Zealand. Part II. – The genus *Odontia*. Transactions of the Royal Society of New Zealand 86(1): 65–103.

Collopy PD, Largeteau-Mamoun ML, Romaine CP, Royse DJ (2001) Molecular phylogenetic analyses of *Verticillium fungicola* and related species causing dry bubble disease of the cultivated button mushroom, *Agaricus bisporus*. Phytopathology 91: 905–912. https://doi.org/10.1094/PHYTO.2001.91.9.905

David A, Rajchenberg M (1992) West African polypores: new species and combinations. Mycotaxon 45: 131–148.

Dueñas M, Telleria MT, Melo I, Martín MP (2009) *Lagarobasidium calongei* (Aphyllophorales, Basidiomycota), a new species of corticioid fungi from Azore Islands. Anales del Jardín Botánico de Madrid 66(S1): 41–46. https://doi.org/10.3989/ajbm.2230

Dvořák D, Vašutová M, Hofmeister J, Beran M, Hošek J, Běťák J, Burel J, Deckerová H (2017) Macrofungal diversity patterns in central European forests affirm the key importance of old-growth forests. Fungal Ecology 27: 145–154. https://doi.org/10.1016/j.funeco.2016.12.003

Eriksson J, Ryvarden L (1976) The Corticiaceae of North Europe Vol. 4, *Hyphodermella – Mycoacia*. Fungiflora, Oslo.

Fernández-Lopéz J, Dueñas M, Martín MP, Telleria MT (2018a) *Xylodon jacobaeus* J. Fernández-López, M. Dueñas, M.P. Martín & Telleria, sp. nov. In: Crous PW, Luangsa-ard JJ, Wingfield MW et al. (2018) Fungal planet description sheets: 785–867. Persoonia 41: 238–417. https://doi.org/10.3767/persoonia.2018.41.12

Fernández-Lopéz J, Martín MP, Dueñas M, Telleria MT (2018b) Multilocus phylogeny reveals taxonomic misidentification of the *Schizopora paradoxa* (KUC8140) representative genome. MycoKeys 38: 121–127. https://doi.org/10.3897/mycokeys.38.28497

Fukami T, Dickie IA, Paula Wilkie PJ, Paulus BC, Park D, Roberts A, Buchanan PK, Allen RB (2010) Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecology Letters 13(6): 675–684. https://doi.org/10.1094/PHYTO.2001.91.9.905

Gafforov Y, Riebesehl J, Ordynets A, Langer E, Yarasheva M, Ghobad-Nejhad M, Zhou LW, Wang XW, Gugliotta AM (2017) *Hyphodontia* (Hymenochaetales, Basidiomycota) and similar taxa from Central Asia. Botany 95(11): 1041–1056. https://doi.org/10.1139/cjb-2017-0115

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. Molecular Ecology 2(2): 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Ginns J, Lefebvre MNL (1993) Lignicolous corticioid fungi (Basidiomycota) of North America: Systematics, distribution, and ecology. Mycologia Memoirs 19: 1–247.

Gorjón SP (2012) Some species of *Hyphodontia* s.l. with encrusted cystidial elements. Mycosphere 3(4): 464–474. https://doi.org/10.5943/mycosphere/3/4/10

Gorjón SP, Greslebin AG (2012) Type studies of the species of *Odontia* described by GH Cunningham. New Zealand Journal of Botany 50(3): 289–301. https://doi.org/10.1080/0028825X.2012.681385

Greslebin AG, Rajchenberg M, Bianchinotti AV (2000) On *Hyphodontia australis* (Corticiaceae, Basidiomycota). Mycotaxon 74(1): 37–43.

Hibbett DS, Binder M (2002) Evolution of complex fruiting-body morphologies in homobasidiomycetes. Proceedings of the Royal Society of London B: Biological Sciences 269(1504): 1963–1969. https://doi.org/10.1098/rspb.2002.2123

Hjortstam K (1987) Studies in tropical Corticiaceae (Basidiomycetes) VIII. Specimens from East Africa collected by L. Ryvarden. II. Mycotaxon 28(1): 19–17.

Hjortstam K (1991) *Athelopsis* instead of *Pteridomyces* (Corticiaceae, Basidiomycetes). Mycotaxon 42: 149–154.

Hjortstam K, Bononi VLR (1987) A contribution to the knowledge of Corticiaceae s.l. (Aphyllophorales) in Brazil. Mycotaxon 28(1): 1–15.

Hjortstam K, Ryvarden L (1980) Studies in tropical Corticiaceae (Basidiomycetes) II. Mycotaxon 12(1): 168–184.

Hjortstam K, Ryvarden L (1984) Some new and noteworthy Basidiomycetes (Aphyllophorales) from Nepal. Mycotaxon 20(1): 133–151.

Hjortstam K, Ryvarden L (2002) Studies in tropical corticioid fungi (Basidiomycota, Aphyllophorales): *Alutaceodontia*, *Botryodontia*, *Hyphodontia* s.s. and *Kneiffiella*. Synopsis Fungorum 15: 7–17.

Hjortstam K, Ryvarden L (2007a) The genus *Palifer*. Synopsis Fungorum 22: 7–10.

Hjortstam K, Ryvarden L (2007b) Studies in corticioid fungi from Venezuela III (Basidiomycotina, Aphyllophorales). Synopsis Fungorum 23: 56–107.

Hjortstam K, Ryvarden L (2009) A checklist of names in *Hyphodontia* sensu stricto – sensu lato and *Schizopora* with new combinations in *Lagarobasidium*, *Lyomyces*, *Kneiffiella*, *Schizopora*, and *Xylodon*. Synopsis Fungorum 26: 33–55.

Hjortstam K, Ryvarden L, Itturiaga T (2005) Studies in corticioid fungi from Venezuela II (Basidiomycotina, Aphyllophorales). Synopsis Fungorum 20: 42–78.

Jang Y, Jang S, Lee J, Lee H, Lim YW, Kim C, Kim JJ (2016) Diversity of wood-inhabiting polyporoid and corticioid fungi in Odaesan National Park, Korea. Mycobiology 44(4): 217–236. https://doi.org/10.5941/MYCO.2016.44.4.217

Jo JW, Kwag YN, Kim NK, Oh SO, Kim CS (2018) A-33: Newly recorded macrofungal species (*Xylodon flaviporus*) in Dokdo, Republic of Korea. KSM Newsletter 30(1): 83–83.

Kan YH, Qin WM, Zhou LW (2017) *Hyphodontia mollissima* sp. nov. (Schizoporaceae, Hymenochaetales) from Hainan, southern China. Mycoscience 58: 297–301. https://doi.org/10.1016/j.myc.2017.04.003

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Kotiranta H, Saarenoksa R (2000) Three new species of *Hyphodontia* (Corticiaceae). Annales Botanici Fennici 37: 255–278.

Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Kwon SL, Jang S, Kim MJ, Kim K, Kim CW, Jang Y, Lim YW, Kim C, Kim JJ (2018) Identification of three wood decay fungi in Yeoninsan Provincial Park, Korea. Journal of Species Research 7(3): 240–247.

Langer E (1994) Die Gattung *Hyphodontia* John Eriksson. Bibliotheca Mycologica 154, J. Cramer, Berlin, Stuttgart, 1–298.

Larsson KH (2007) Re-thinking the classification of corticioid fungi. Mycological Research 111(9): 1040–1063. https://doi.org/10.1016/j.mycres.2007.08.001

Larsson KH (2014) Nomenclatural novelties. Index Fungorum 131: 1.

Larsson KH, Larsson E, Kõljalg U (2004) High phylogenetic diversity among corticioid homobasidiomycetes. Mycological Research 108(9): 983–1002. https://doi.org/10.5941/MYCO.2016.44.4.217

Larsson KH, Parmasto E, Fischer M, Langer E, Nakasone KK, Redhead SA (2006) Hymenochaetales: a molecular phylogeny for the hymenochaetoid clade. Mycologia 98(6): 926–936. https://doi.org/10.3852/mycologia.98.6.926

Nilsson RH, Tedersoo L, Abarenkov K, Ryberg M, Kristiansson E, Hartmann M, Schoch CL, Nylander JAA, Bergsten J, Porter TM, Jumpponen A, Vaishampayan P, Ovaskainen O, Hallenberg N, Bengtsson-Palme J, Eriksson KM, Larsson KH, Larsson E, Kõljalg U (2012) Five simple guidelines for establishing basic authenticity and reliability of newly generated fungal ITS sequences. MycoKeys 4: 37–63. https://doi.org/10.3897/mycokeys.4.3606

Nordén B, Appelquist T, Lindahl B, Henningsson M (1999) Cubic rot fungi – corticioid fungi in highly brown rotted spruce stumps. Mycologia Helvetica 10(2): 13–24.

Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University. https://github.com/nylander/MrModeltest2

O'Donnell K (1993) *Fusarium* and its near relatives. In: Reynolds DR, Taylor JW (Eds) Fungal systematics; the fungal holomorph: mitotic, meiotic and pleomorphic speciation. CAB International, Wallingford, 223–225.

Paulus B, Hallenberg N, Buchanan PK, Chambers GK (2000) A phylogenetic study of the genus *Schizopora* (Basidiomycota) based on ITS DNA sequences. Mycological Research 104(10): 1155–1163. https://doi.org/10.1017/S0953756200002720

Persoon CH (1801) Synopsis methodica fungorum. Vol 1. Henrich Dieterich Publ., Gottingae.

Povah AH (1929) Some non-vascular cryptogams from Vermillion, Chippewa County, Michigan. Papers Mich. Acad. Sci., Arts and Letters 9: 253–272.

Rambaut A (2012) FigTree v1.4. http://tree.bio.ed.ac.uk/software/figtree [Accessed 5 December 2012]

Riebesehl J, Langer E (2017) *Hyphodontia* s.l. (Hymenochaetales, Basidiomycota): 35 new combinations and new keys to all 120 current species. Mycological Progress 16(6): 637–666. https://doi.org/10.1007/s11557-017-1299-8

Riebesehl J, Langer EJ, Ordynets A, Striegel MM, Witzany C (2015) *Hyphodontia borbonica*, a new species from La Réunion. Mycological Progress 14: 104. https://doi.org/10.1007/s11557-015-1126-z

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19(12): 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Rosenthal LM, Larsson KH, Branco S, Chung JA, Glassman SI, Liao HL, Peay KG, Smith DP, Talbot JM, Taylor JW, Vellinga EC, Vilgalys R, Bruns TD (2017) Survey of corticioid fungi in North American pinaceous forests reveals hyperdiversity, underpopulated sequence databases, and species that are potentially ectomycorrhizal. Mycologia 109(1): 115–127. https://doi.org/10.1080/00275514.2017.1281677

Stalpers J, Buchanan PK (1991) Type studies of the species of *Pellicularia* and *Peniophora* described by G. H. Cunningham. New Zealand Journal of Botany 29: 331–340. https://doi.org/10.1080/0028825X.1991.10416611

Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10(3): 512–526.

Ţura DA, Zmitrovich IV, Wasser SP, Spirin WA, Nevo E (2011) Biodiversity of the Heterobasidiomycetes and non-gilled Hymenomycetes (former Aphyllophorales) of Israel. Gantner Verlag K-G, Ruggell, 1–566.

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172(8): 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Viner I, Spirin V, Zíbarová L, Larsson KH (2018) Additions to the taxonomy of *Lagarobasidium* and *Xylodon* (Hymenochaetales, Basidiomycota). MycoKeys 41: 65–90. https://doi.org/10.3897/mycokeys.41.28987

Wang M, Chen YY (2017) Phylogeny and taxonomy of the genus *Hyphodontia* (Hymenochaetales, Basidiomycota) in China. Phytotaxa 309(1): 45–54. https://doi.org/10.11646/phytotaxa.309.1.4

Wang Y, Lai Z, Li XX, Yan RM, Zhang ZB, Yang HL, Zhu D (2016) Isolation, diversity and acetylcholinesterase inhibitory activity of the culturable endophytic fungi harboured in *Huperzia serrata* from Jinggang Mountain, China. World Journal of Microbiology and Biotechnology 32(2): 1–23. https://doi.org/10.1007/s11274-015-1966-3

White TJ, Bruns TD, Lee SB, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR protocols: a guide to methods and applications. Academic Press, New York, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wu SH (1990) The Corticiaceae (Basidiomycetes) subfamilies Phlebioideae, Phanerochaetoideae and Hyphodermoideae in Taiwan. Acta Bot. Fennica 142: 1–123.

Xiong HX, Dai YC, Wu SH (2010) Two new species of *Hyphodontia* from China. Mycologia 102(4): 918–922. https://doi.org/10.3852/09-139

Yombiyeni P, Douanla-Meli C, Amalfi M, Decock C (2011) Poroid Hymenochaetaceae from Guineo-Congolian rainforest: *Phellinus gabonensis* sp. nov. from Gabon – taxonomy and phylogenetic relationships. Mycological Progress 10(3): 351–362. https://doi.org/10.3852/14-298

Yurchenko E, Riebesehl J, Langer E (2017) Clarification of *Lyomyces sambuci* complex with the descriptions of four new species. Mycological Progress 16(9): 865–876. https://doi.org/10.1007/s11557-017-1321-1

Yurchenko E, Wu SH (2014) Three new species of *Hyphodontia* with peg-like hyphal aggregations. Mycological Progress 13(3): 533. https://doi.org/10.1007/s11557-013-0935-1

Yurchenko E, Xiong HX, Wu SH (2013) Four new species of *Hyphodontia* (*Xylodon* ss. Hjortstam & Ryvarden, Basidiomycota) from Taiwan. Nova Hedwigia 96(3–4): 545–558. https://doi.org/10.1127/0029-5035/2013/0092

Zhao CL, Cui BK, Dai YC (2014) Morphological and molecular identification of two new species of *Hyphodontia* (Schizoporaceae, Hymenochaetales) from southern China. Cryptogamie Mycologie 35(1): 87–97. https://doi.org/10.7872/crym.v35.iss1.2014.87